Behavioral and Physiological Effects in Capercaillie *(Tetrao urogallus)* Caused by Human Disturbance

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Dissertation

zur

Erlangung der naturwissenschaftlichen Doktorwürde

(Dr. sc. nat.)

vorgelegt der

Mathematisch-naturwissenschaftlichen Fakultät

der

Universität Zürich

von

Dominik Karl THIEL

von

Zollikon/ZH

Promotionskomitee

Prof. Dr. Bernhard Schmid (Vorsitz)
PD Dr. Lukas Jenni (Leiter der Dissertation)
Dr. Susanne Jenni-Eiermann
Prof. Dr. Christine B. Müller
Prof. Dr. Rupert Palme
Prof. Dr. Ilse Storch

Zürich 2007

Die vorliegende Arbeit wurde von der Mathematisch-naturwissenschaftlichen Fakultät der Universität Zürich am 05.02.2007 als Dissertation angenommen.

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Summary

Outdoor recreation is of great conservation concern and has been documented as a cause for population decline in several species. Free-ranging animals often respond to the occurrence of humans by an antipredatory behavior. Depending on the frequency and the strength of such responses, individual fitness can be negatively affected. Multi-methodological approaches are necessary to better understand how human recreation affects free-ranging animals and to create effective management plans where areas of recreation activities overlap with the occurrence of endangered species.

The capercaillie (*Tetrao urogallus*) is a rare and shy forest grouse with specific habitat requirements. The decline of populations in areas with increasing human outdoor activities has led to the assumption that capercaillie are negatively affected by human disturbance. However, studies investigating the individual response of capercaillie to human disturbance are lacking. In this thesis, we investigated behavioral and physiological responses of capercaillie to winter recreation to determine their susceptibility to human disturbance.

First, we investigated the metabolism of corticosterone, the excretion pattern of its metabolites in capercaillie droppings, and validated a suitable method to measure stress hormone levels in droppings of free-ranging capercaillie (paper I). Then, we studied night roost selection in several central European capercaillie populations to improve the knowledge on winter ecology (paper II). Further, we investigated the individual behavioral response of capercaillie to various winter recreation intensities by measuring flushing distances (paper III) and habitat use of radio-tracked capercaillie (paper IV). Stress hormone levels in droppings sampled in undisturbed and disturbed populations were compared to study the physiological stress response (paper IV and V).

Night roost selection was determined by strategies aiming to save energy and avoid predators. Behavior and stress physiology of capercaillie were affected by winter recreation. The extent of these responses to winter recreation depended on the temporal and spatial scale. Capercaillie in areas with high winter recreation intensities exhibited longer flushing distances and higher stress hormone levels than birds in undisturbed sites. Before the beginning of the ski season, habitat use within home ranges was not affected by recreation intensity. Capercaillie did not shift their home ranges with the beginning of the ski season. However, capercaillie avoided highly disturbed areas within their home ranges during the ski season. Females tended to respond less strongly to disturbances than males.

Our results suggest that capercaillie are in an energetically critical situation during winter. Disturbance-caused stress responses may lead to additional energy expenditure and fitness costs. Therefore we believe that capercaillie in winter are highly susceptibly to human disturbance. We recommend to restrict winter outdoor recreation activities in capercaillie core areas to trails, ski-runs and ski-tracks as predictable disturbance sources. Where capercaillie occur in areas with human recreation activities, such recreation areas should be interspersed with disturbance-free areas by establishing officially declared wildlife refuges with prohibited human access.

Zusammenfassung

Der Freizeittourismus hat in der Naturschutzbiologie an Bedeutung gewonnen, und gilt für verschiedene Arten als Verursacher von Bestandesrückgängen. Wildtiere reagieren beim Erscheinen von Menschen oft mit einem Räuber-Vermeidungsverhalten. Je nach der Häufigkeit und der Stärke einer solchen Verhaltensreaktion kann die individuelle Fitness der Wildtiere negativ beeinträchtigt werden. Um den Einfluss von Freizeittourismus auf Wildtiere besser verstehen zu können, und um Aktionspläne für bedrohte Arten in Gebieten mit menschlichen Freizeitaktivitäten erfolgreich umzusetzen, ist die Anwendung von verschiedenen Untersuchungsmethoden notwendig.

Das Auerhuhn (*Tetrao urogallus*) ist ein seltenes und scheues waldbewohnendes Raufusshuhn mit hohen Ansprüchen an seinen Lebensraum. Bestandesrückgänge dieser Art in Gebieten mit zunehmendem Tourismusbetrieb haben zur Annahme geführt, dass das Auerhuhn unter menschlichen Störungen leidet. Es fehlen jedoch Studien wie Auerhühner auf Individuenebene auf menschliche Störungen reagieren. In dieser Doktorarbeit haben wir untersucht wie Auerhühner verhaltensbiologisch und physiologisch auf den Freizeittourismus im Winter reagieren, um die Störungsempfindlichkeit des Auerhuhns auf menschliche Störungen zu bestimmen.

Als erstes haben wir den Metabolismus von Kortikosteron und das Ausscheidungsmuster der Kortikosteron-Metaboliten im Auerhuhnkot untersucht, und validierten eine Methode, um den Stresshormonlevel in Kotproben freilebender Auerhühner zu messen (Paper I). Als nächstes untersuchten wir die Muster der Schlafplatzauswahl in verschienen Auerhuhnpopulationen Mitteleuropas, um das Wissen über die Winterökologie dieses Huhns zu vergrössern (Paper II). Im weiteren erforschten wir die individuelle Verhaltensantwort von Auerhühnern in Abhängigkeit von verschiedenen Intensitäten von Wintertourismus, indem wir Fluchtdistanzen gemessen haben, und die Lebensraumnutzung besenderter Auerhühner untersuchten (Paper IV). Die physiologische Stressantwort wurde durch den Vergleich von Stresshormonlevels in Kotproben aus unterschiedlich stark gestörten Populationen untersucht (Paper IV und V).

Auerhühner wählen ihre Schlafplätze um möglichst gut Energie sparen- und Prädatoren vermeiden zu können. Das Verhalten und die Stressphysiologie der Auerhühner wurden durch den Wintertourismus klar beeinflusst. Die Stärke dieser Stressantworten auf den Wintertourismus waren jedoch zeit- und raumspezifisch. Auerhühner in Gebieten mit starkem Freizeitbetrieb wiesen höhere Fluchtdistanzen und höhere Stresshormonlevels auf als ihre Artgenossen in wenig belasteten Gebieten. Das Homerange wurde mit dem Beginn der Skisaison nicht verschoben, Auerhühner mieden jedoch stark gestörte Gebiete innerhalb ihres Homeranges während der Skisaison. Die Reaktionen von Hennen auf Störungen waren tendenziell schwächer als jene der Hähne.

Unsere Resultate weisen darauf hin, dass sich Auerhühner im Winter in einer kritischen energetischen Situation befinden. Störungsverursachte Stressreaktionen können zu zusätzlichen Energie- und Fitnesskosten führen. Wir vermuten, dass Auerhühner im Winter deshalb besonders störungsanfällig sind. Wir empfehlen Freizeitaktivitäten im Winter in Auerhuhn-Kerngebieten auf für Wildtiere vorhersehbare Störungsquellen wie Wege, Skipisten und Langlaufloipen zu beschränken. Dort, wo Auerhühner in touristisch genutzten Gebieten vorkommen, sollten ausgewiesene störungsfreie Wildruhezonen mit Zutrittsverboten geschaffen werden.

General introduction

Motivation and state of the art

With the increase of human mobility and the desire of many people to recreate in nature, human leisure activities are becoming more and more numerous and widespread. With a variety of outdoor sport activities (snow-shoeing, paragliding, canyoning, river-rafting), more and more so far untouched and pristine wildlife habitats become affected by humans. In addition to sport activities, ecotourism including 'wildlife watching' such as visiting seabird or penguin colonies rapidly increased worldwide (Ceballos-Lacurain 1996). Recreation tourism is a substantial economic factor for instance in the Alps (Elsasser & Messerli 2001), and the expenses for recreation have increased.

Studies investigating the effects of human disturbance have increased in numbers over the last decade, because human disturbance is a documented cause of population decline in endangered species (Venizelos 1991), and the fourth leading cause for the decline of federally threatened and endangered species in the United States (Czech 2000). New questions have become of great conservation concern (Gill, Norris & Sutherland 2001a): how does wildlife respond to recreation activities, can wildlife habituate to human disturbances, and what are the effects of recreation activities on free-living animals? The theory to better understand and predict the effects of human-induced disturbances on animals was recently rediscovered and confirmed by Frid & Dill (2002) and Beale & Monaghan (2004): animals perceive humans as predators, and respond to their appearance with an anti-predatory behavior. An example demonstrating this theory are species evolved on islands without predators which almost lack a response to the presence of humans such as the kakapo (*Strigops habroptilus*) in New Zealand. Predation and human disturbance stimuli create similar trade-offs between avoiding the perceived risk and other fitness-enhancing activities (feeding, mating, parental care). Responses to predation risk and disturbance stimuli both divert time and energy from other fitness-related activities, and this trade-off has to be optimized. Stillmann & Goss-Custard (2002) found such a trade-off in Oystercatchers (*Haematopus ostralegus*): their behavioral response to disturbance is less strong in late winter when food is scarce and hence their starvation risk when avoiding disturbance is greater than in early winter when food is abundant.

In contrast to other human activities such as urban sprawl or land use (agriculture, forestry), most outdoor leisure activities do not modify habitats. In the context of this study, human disturbance is defined as the deviation from the normal and preferred behavior of free-living animals by the occurrence of humans (Boere 1975; Platteeuw & Henkens 1997). The European commission defines disturbances as "any phenomenon that may cause a significant change in the dynamics of a population or the eco-ethological characteristics of populations" (cited in Harradine 1998), which expands the scale from individuals to populations.

Wildlife reacts to human disturbances with behavioral and physiological responses. Behavioral responses include a.o. changes in daily activity budget (Pedroli 1983), habitat use (Gill, Norris & Sutherland 2001b), choice of nesting and roosting sites (Knight & Fitzner 1985) and alert and flee behavior (Fernandez-Juricic, Jimenez & Lucas 2002). Then, in turn animals try to compensate for human-induced changes by lengthening the time of feeding (Urfi, Goss-Custard & Durell 1996), by increasing digestion capacity (Swennen, Leopold & de Bruijn 1989), or by increasing the resting time

(Duchesne, Coté & Barrette 2000). Animals can physiologically respond to the occurrence of humans with changes of the cardiovascular system (Cabanac & Guillemette 2001; Weimerskirch et al. 2002) and /or levels in circulating stress hormones. The latter includes an activation of the hypothalamo-pituitary-adrenal axis and the secretion of glucocorticoid hormones into the blood (Sapolsky, Romero & Minck 2000), as a mechanism to adjust the behaviour and the physiology of the animal to prevailing environmental conditions (Wingfield & Romero 1999). Several studies demonstrated that a physiological response to human disturbance can occur while no behavioural response is apparent, and vice versa (Eilam et al. 1999; Walker, Boersma & Wingfield 2005; Müller et al. 2006).

As a consequence of such a behavioral and/or physiological response, predation risk, energy expenditure (Cassirer 1992), energy intake and therefore body condition (Schnidrig-Petrig & Ingold 2001) and survival (Müllner, Linsenmair & Wikelski 2004) can be negatively affected. Moreover, chronically elevated and prolonged high levels of corticosterone can affect immune function, growth, reproduction and survival (Wingfield 1994; Lucas et al. 2006).

Most studies investigated effects of human disturbance at the level of individuals (behaviour, physiology), only few studies on populations or community structures (see review in Keller 1995). Anyway, the type and strength of such a response can vary with the frequency and the predictability of disturbances. Habituation to unpredictable disturbances is difficult (Whittaker & Knight 1998; Miller, Knight & Miller 2001). In addition, the type and strength of such a response depend on modulating factors. Animals may react differently depending on species, sex, age, season, body condition, reproductive status, genetic predisposition, past experiences or habituation. Therefore, studies need to consider these modulating factors, and should also carefully select a suitable method to measure potential effects of disturbances.

While some species seem to support the presence of humans easily such as penguins (Walker, Boersma & Wingfield 2006), others seem to be very sensitive. The capercaillie (*Tetrao urogallus*) probably belongs to the second group of species. They are supposed to be especially susceptible for human disturbance (Klaus et al. 1989). Even though the large scale distribution range of capercaillie in Eurasia did not markedly change in the last decades and the birds still inhabit most of the former area, populations in western and central Europe significantly declined in the last decades (Storch 2000). In most European countries, capercaillie are nowadays endangered or threatened. Habitat loss and fragmentation have resulted in small populations with a high risk of extinction (Storch 2000; Storch 2007). Capercaillie numbers in Switzerland approximately halved within the last three decades (Mollet et al. 2003), and self-sustaining populations in Germany only survived in the Black Forest and in the Bavarian Alps. Capercaillie are expected to be especially susceptible and affected to human disturbance for the following reasons: (1) Capercaillie have specific habitat preferences and large spatial requirements. Therefore, suitable habitats may not be available if they once dislocate as a response to human recreation. (2) Capercaillie are large and heavy birds; alert und flushing distances increase with body size (Blumstein et al. 2005), and thus entail more frequent fleeing for capercaillie than for small animals. (3) The capercaillie is a prey species of several aerial and terrestrial predators (Gjerde & Wegge 1989). Since humans are perceived as predators, they have a pronounced flee behavior. (4) Most recreation activities in capercaillie habitats are conducted in winter (skiing, snow-shoeing, dog-sledging e.g.). Winter is the most critical season of the year with high

energy demands. However, energy intake of capercaillie in winter is limited due to the low energy content of conifer needles, the only winter food for capercaillie (Moss & Hansson 1980; Lindén 1984). Although the manifold behavioural, physiological and morphological adaptations of capercaillie to survive under hard environmental conditions, any additional energy expenditure can lead to critical fitness costs.

Although capercaillie received great attention and interest since centuries from hunters, artists, poets, naturalists and scientists, knowledge about effects of human recreation is mainly lacking. Only a few case studies documented a decline or extinction of a local population after the construction or enlargement of ski-facilities (Labigand & Munier 1989; Brenot, Catusse & Ménoni 1996). However, there is a need for scientific-based knowledge how capercaillie are affected by human recreation in order to establish effective conservation management plans as a contribution to stop population declines. This is especially mandatory since most of the remaining isolated capercaillie populations in central Europe (Scotland, France, Germany, Italy, Switzerland, Spain, Austria) inhabit areas that are extensively used for human recreation activities.

Research questions

The lack of a profound knowledge of the effects of disturbance on capercaillie motivated me to start this study. Thereby, I wanted to use several approaches and focus on possible sex-differences in response to human recreation, and to study several central and western European capercaillie populations in various forest types affected by various recreation activities. The methods used should be non-invasive or at least aim at reducing negative effects of research activities. Because population studies are very difficult, I wanted to focus on an individual level. The overall goal of this PhD thesis was to investigate behavioral and physiological effects of human recreation activities in winter on capercaillie. Within this study, it was not possible to investigate possible fitness consequences of human disturbance.

In particular, the objectives of this PhD thesis were:

1) to analyze certain aspects of habitat selection of capercaillie at the individual level:
   What are the characteristics and requirements of capercaillie night roosts in winter, and which factors determine the selection of winter night roosts?

   Are there differences in the selection of winter night roosts and home range sizes between sexes and as winter progresses?

2) to investigate effects of winter recreation on the behavior of capercaillie:
   Does human recreation affect flushing distance of capercaillie?

   Does human winter recreation affect habitat use of capercaillie and are the effects dependent on the spatial scale?

3) to investigate effects of winter recreation on physiological stress in capercaillie:
Are stress hormone levels of capercaillie affected by human winter recreation, and do they differ between sexes?

How are stress hormone levels affected by spatially and temporally varying human winter recreation activities?

Thesis structure

This PhD thesis was part of a large cooperation research project on capercaillie in the Black Forest/Germany to evaluate a habitat model at a landscape scale as a tool for conservation planning (Forest Research Institute of Baden-Württemberg FVA), to examine the dispersal of capercaillie females (Max Planck Institute for Ornithology, Vogelwarte Radolfzell), and to study the susceptibility of capercaillie to human disturbance (Swiss Ornithological Institute).

Paper I: Measuring corticosterone metabolites in droppings of capercaillies (*Tetrao urogallus)*

In a first step, we evaluated a method to measure corticosterone metabolites in capercaillie droppings, since this has never been done before. Therefore, we evaluated the temporal excretion pattern and characterized the stress hormone metabolites in droppings. Then, we validated an enzyme immunoassay to quantify the excreted metabolites, and investigated the stability of these metabolites in droppings among various storage conditions. We did this study with captive capercaillie at the Vogelwarte Radolfzell, and cooperated with the Institute of Biochemistry, Department of Natural Sciences, University of Veterinary Medicine in Vienna.

Paper II: Selection of night roosts in winter by capercaillie *Tetrao urogallus* in Central Europe

Then, we characterized capercaillie winter night roosts and investigated whether there are any preferences for certain roosts by comparing used night roost trees with matched control trees. Data were sampled in the Black Forest (Germany), the Swiss Jura, the Swiss Alps and the Thuringia Forest (Germany) to include a wide range of different forest types. We expected to better understand the various constraints for capercaillie during night roosting, which could give us hints on possible responses to human recreation. Is it microclimate, predation risk or foraging which determines night roost selection?

Paper III: Effects of recreation and hunting on flushing distance in capercaillie

In a further step, we aimed at investigating how capercaillie individuals react to the occurrence of a recreationist. We measured flushing distances as a widely used measure of a local-scale and immediate behavioral disturbance response, where measurements of alert distances or other behavioral responses are impossible due to a bad observability in forests (Blumstein et al. 2003). For this study we investigated recreation intensity and hunting pressure as determinants of flushing

distances. We cooperated with the Office National de la Chasse et de la Faune Sauvage in the French Pyrenees to improve the international relevance of this study. With these results, we expected to quantify areas influenced by disturbances and to create and justify species-specific regulations for recreationists in capercaillie winter core areas.

Paper IV: Ski tourism affects habitat use and evokes physiological stress in capercaillie *Tetrao urogallus*

One major goal of this thesis was to study the effect of ski tourism on habitat use at different spatial scales, and to compare these results with simultaneous measurements of physiological stress in the same individuals. For this study, we radio-tracked capercaillie males and females in one focus population in the Black Forest/Germany. For the stress hormone analyses, we sampled droppings from these individually radio-tracked birds and from additional individuals. The aim was to compare behavioral and physiological responses between temporally and spatially varying winter recreation intensities.

Paper V: Evidence for physiological stress in capercaillie *Tetrao urogallus* due to human winter recreation

Since a physiological stress response to human disturbance could vary among different populations depending on ecological conditions (elevation, food, predators), recreation pressure and types of recreation activities, we enlarged the study to a wider geographical range. We sampled and analyzed capercaillie droppings from some hundred individuals from various capercaillie populations in the Black Forest/Germany, in the Swiss Jura and in the Swiss Alps.

The results of this thesis provided first insights on the effects of human recreation on capercaillie individuals using multiple methods and conducted in many free-living capercaillie populations in western and central Europe. An overall discussion, conclusions and methodological aspects are treated in a synthesis chapter.

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Paper I

Measuring Corticosterone Metabolites in Droppings of Capercaillies (*Tetrao urogallus)*

Published as:

Dominik Thiel[1, 2], Susanne Jenni-Eiermann[1], and Rupert Palme[3]. (2005) Measuring Corticosterone Metabolites in Droppings of Capercaillies (*Tetrao urogallus)*. Annals of the New York Academy of Sciences 1046: 96-108.

[1]Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

[2]Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

[3]Institute of Biochemistry, Department of Natural Sciences, University of Veterinary Medicine, Veterinärplatz 1, A-1210 Vienna, Austria

Abstract

The Capercaillie (*Tetrao urogallus*), the largest grouse species in the world, is decreasing in numbers in major parts of its distribution range. As a possible reason for its decline, disturbances by human outdoor activities are discussed. An indicator for disturbances is the increase of the glucocorticoid corticosterone, a stress hormone, which helps to cope with life threatening situations. However, repeated disturbances might result in a long-term increase of the basal corticosterone concentration, which detrimental effects like reduced fitness and survival of an animal. In order to measure corticosterone metabolites (CM) noninvasively in the droppings of free-living Capercaillies, we first had to select and validate an enzyme immunoassay (EIA) in captive birds. Therefore excretion pattern of intravenously injected radiolabeled corticosterone were determined and ^{3}H-metabolites were characterised. High-performance-liquid-chromatography (HPLC) separations of the samples containing peak concentrations revealed that corticosterone was extensively metabolised. The HPLC fractions were tested in several EIAs for glucocorticoid metabolites. The physiological relevance of this method was proven after pharmacological stimulation of the adrenocortical activity. Only the recently established cortisone assay, measuring CM with a 3,11 dione structure detected an expressed increase of concentrations following ACTH stimulation. To set up a sampling protocol

suited for the field, we examined the influence of various storage conditions and time of day on concentrations of CMs.

Introduction

The Capercaillie (*Tetrao urogallus*), the largest Galliform bird species in the Palearctic, is decreasing in numbers in most parts of its distribution range.[1] This decrease is particularly strong in Central Europe, where many populations are already extinct or threatened with extinction.[2] Consequently, the Capercaillie is classified as endangered species on the Red List of Switzerland[3] and as critically endangered in Germany[4] and Austria.[5] In Switzerland numbers of Capercaillie were reduced to less than half during the last 30 years and the decline is still going on.[6] The decrease is mainly caused by habitat loss and habitat degradation.[2,6,7] The decline of the Capercaillie in areas with increasing human outdoor activities has lead to the assumption that Capercaillies are negatively affected by human disturbance.[2,8] Firstly, human presence may lead to the avoidance of the disturbed area and to a change into a habitat of lower quality, a reaction which may negatively affect survival[9], as was suggested for the Capercaillie in Germany.[10] Secondly, human induced disturbance can have significant energetic consequences, particularly during winter, and may disturb the normal activity pattern and cause an energy deficit, as was shown for Snow Geese (*Chen caerulescens*[11]). If prolonged or repeated, human disturbance causes repeated physiological stress reactions, which may result in long-term negative effects, such as a reduced reproduction or a reduced immuncompetence.[12,13] However, in the Black Forest (Germany) some Capercaillies live close to paths, ski trails or ski runs.[14] Whether these birds are stressed or whether they are adapted to human encounters is not known.

A possibility to find out, whether an individual shows physiological stress reactions, even in the absence of an obvious behavioral response, is to analyse the amounts of stress hormones released. The organism reacts to stress with the activation of the hypothalamo-pituitary–adrenal axis, resulting in a release of glucocorticoids (in birds: corticosterone) into the blood, which triggers adjustments in physiology and behavior to help the organism to survive.[13,15] Plasma glucocorticoid concentrations are therefore widely used to diagnose a physiological stress response.[16,17,18,19]

In free-living Capercaillies it is impossible to sample blood without causing severe stress by capture and handling. Therefore, the non-invasive method to quantify hormone production by the measurement of the hormone metabolites excreted in droppings collected in the field offers the possibility to track the metabolic response to disturbances.[20] Since this method is feedback-free, repeated measurements are possible in the same individual.[21]

CM in droppings have been quantified in a few avian species. [22,23,24,25,26,27,28] Glucocorticoids are extensively metabolized before excretion and native corticosterone was not found in the droppings.[28] The metabolism of corticosterone varies between species (and even gender) and therefore the best suited immunoassay has to be chosen and the method validated for each species anew. [29, 30] When using droppings from a free-living species, additional studies are necessary to assess whether the particular sampling conditions in the field, often suboptimal, affect the concentration of corticosterone metabolites (CM) in the droppings. Because of the low densities and the cryptic behavior, Capercaillies can not be followed and observed easily.[8] Droppings cannot be

collected shortly after defecation and, therefore, the exact time of defecation in droppings found in the field is unknown. Therefore, it needs to be evaluated whether and under which ambient conditions CM degrade after voidance[31,32] and whether the excretion of CM varies over the day[33].

The aim of this study was thus to select and validate an enzyme immunoassay (EIA) for the quantification of CM in Capercaillie droppings collected in the field and to test the influence of various storage conditions. This was done by the following steps: In a radiometabolism study, the excreted CM were characterized with reversed-phase high-performance liquid chromatography (RP-HPLC). Subsequently, several antibodies were tested to select the best suited EIA for their quantification. Finally, the method was physiologically validated by inducing a corticosterone release through an ACTH (adrenocorticotropic hormone) injection. Experimentally, we tested the influence of time of day, temperature and duration of storage on the concentration of CM in droppings. This procedure is in accordance with the guidelines recommended.[34]

Material and methods

Animals

All experiments with Capercaillies (*Tetrao urogallus*) were conducted with captive birds in the Max-Planck-Institute for Ornithology, Radolfzell, Germany. The birds were housed in outdoor aviaries, exposed to natural light and temperature conditions, but protected from precipitation. Each aviary had one male, while the much smaller females could freely move between aviaries through small openings. During the cold season, the period when we did our experiments, the birds were supplied with water, conifer needles and maize *ad libitum*. The age of the birds was at least one year. Body mass ranged between 3 - 4 kg in males and 1.5 - 2 kg in females.

For the experiments, birds were transferred singly to aviaries of $3 \times 3 \times 2.5$ m. Their floor was covered with a plastic sheet, so that droppings could be easily collected and the floor could be cleaned. Capercaillies feeding on needles and maize void brown, nearly nitrogen-free, dry and compact droppings.[35,36] One female reacted very nervous when the aviary was entered for sampling droppings during the radiometabolism study and it voided more liquid droppings. The droppings of the ceca, which are of a pasty consistency, a different shape and a penetrating odor, were not sampled. They are voided only once per day, are hard to find in the field and decay within a few days under frozen conditions.

Radiometabolism study

The experiment was carried out during 13 - 16 April 2003. The day before the experiment, two males and two females were placed in separate aviaries to ensure that the droppings were not mixed up. The next day at 8 am each bird was injected with 1.85 MBq (=50 µCi) of radiolabeled corticosterone ([1,2,6,7,- ^{3}H(N)]-corticosterone; specific activity 76.5 Ci/mmol, Perkin Elmer Life Sciences, Boston, USA) dissolved in 0.5 ml 0.9% NaCl solution containing 10% ethanol into the *Vena ulnaris*.

One hour before injection, droppings of each bird were collected to determine background levels of radioactivity. During the first day after injection, droppings were collected every hour until 23 pm and frozen immediately at –23°C. Thereafter they were collected every second hour until 7 am. During the

second day after injection, droppings were collected in 3 hour intervals until 5 pm and during the third and fourth day at 8 am, 13 pm and 6 pm.

Radioactivity in the droppings was measured as described earlier.[28] Briefly, 0.5 g of the homogenized sample were extracted with 5 ml of 60% methanol by shaking for 30 min. After centrifugation, aliquots (0.5 ml in duplicates) of the supernatant were mixed with 6 ml of a scintillation fluid (Quicksafe A®, No 100800, Zinsser Analytic, Maidenhead, UK) and measured in a liquid scintillation counter (Packard Tri-carb 2100TR, Meriden, CT, USA). Radioactivity was expressed as kilobecquerels (kBq) per kg of sample.

To characterize the excreted metabolites, RP-HPLC separations were performed with the samples containing the highest amounts of radioactive metabolites. Clean-up and separations are described previously. [28,33,37]

Analysis of metabolites

The immunoreactivity of the 90 fractions eluted from the RP-HPLC (diluted 1:5 with assay buffer) was measured in different EIAs. Three assays were tested: an 11-oxoetiocholanolone-[38], a cortisone-[28] and a 20β-dihydrocorticosterone-EIA[39]. EIAs were performed as described previously[40] on microtiter plates coated with anti-rabbit immunoglobulin G (IgG) using a double antibody technique and biotinylated steroids as labels.

Administration of ACTH

The physiological relevance of the method was evaluated by stimulating adrenocortical activity with ACTH. Three males and two females were injected with 1 ml (0.25 mg) of ACTH (Synacthen®, Novartis Pharma Schweiz SA, Bern) in the *vena ulnaris.*

Experiments were conducted during 13 - 16 April 2003 (1 male, 1 female), and during 8 - 12 February 2004 (2 males, 1 female). To obtain basal values, droppings were collected one hour before injection. After injection, droppings were collected for four days, the first 48 hours once per hour, thereafter sampling frequency was gradually reduced down to 3 times per day on the last day. In 2004, droppings were also collected over 28 h before injection in order to assess the diurnal rhythm of CM in droppings.

All samples were immediately stored at -23ºC until analysis. The samples were extracted as described above, except the 2004 samples, which were lyophilised before extraction. According to the water loss of lyophilisation a reduced weight of sample was used for the extraction. Results were expressed in nmol/kg fresh weight. The aliquots of the supernatant (diluted 1:10 with assay buffer) were measured with the cortisone–EIA and the 11-oxoetiocholanolone-EIA[28,38] to determine the amounts of CM in the droppings.

Effect of storage duration, temperature and gender on CM

Droppings were collected in 3 different aviaries within 24 hours after cleaning the floor, each holding 1 male but several females freely moving between the aviaries. Therefore only male droppings were individual-specific. 100 g of the droppings of each gender and aviary were pooled, homogenized and divided into subsamples of 0.5 g each. 15 samples of each gender and aviary were frozen

immediately. 5 samples of each gender and aviary were stored at 8°C for 1, 7 and 21 days, respectively, and another 5 samples of each gender and aviary at 21°C for 1, 7 and 21 days, respectively. CM were analyzed following the procedure described above.

We tested for effects of these factors on log10-transformed values of CM in a split-plot ANOVA[41] with individuals nested within aviaries and single portions of droppings nested within individuals. Since gender varies among individuals, it is tested against the residual variation among individuals within aviaries. All other factors including interactions vary among portions of droppings and are therefore tested at the lowest level of the experiment, i.e. using the residual mean square, which quantifies the variation among portions of droppings nested within individuals. To test the significance of particular group differences, we compared them with the least significant difference at an alpha level of 5%. Analysis was conducted using the GenStat package.[42]

Results

Radiometabolism study

Excretion of ^{3}H-corticosterone started immediately, as above-background radioactivity was measured in the first droppings collected 1 h after injection. All four birds had one main peak, followed by some smaller peaks. The radioactivity returned to background levels about 33 h after injection. Three individuals showed a broad peak between 1 and 4 h after injection (Fig. 1). Female B differed from the other three birds by showing one sharp peak of radioactivity 1 h and a second lower and broader peak 3 - 4 h after injection. This female was quite nervous and was the only bird with more liquid droppings (see Material and Methods).

The RP-HPLC separations of the droppings with the highest radioactivity revealed the presence of 3 - 4 major radioactive peaks (mainly between fractions 30 to 50) and a large number of smaller peaks indicating that several CM were excreted (Fig. 2). Only negligible (if at all) amounts of radioactivity eluted at the position of corticosterone. In the HPLC fractions, highest amounts of immunoreactivity were detected with the cortisone-EIA, measuring metabolites with a common 3,11-dione structure, and the 11-oxoetiocholanolone assay, measuring CM with a 5β-3α-11-one structure (Fig. 2a and b).

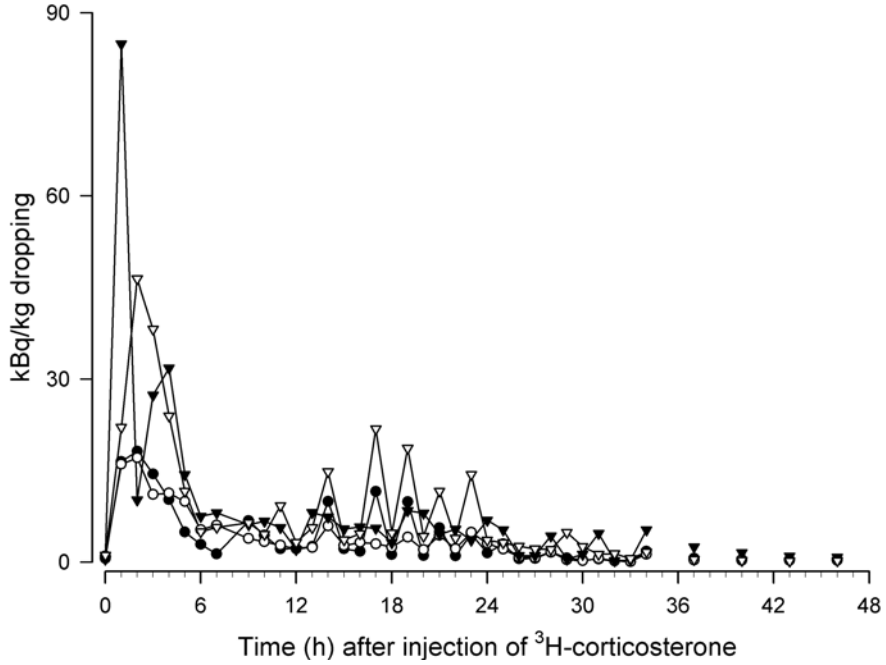

Figure 1. *Time course of excretion of ^{3}H-corticosterone in droppings of 2 male and 2 female Capercaillies. The circles represent the two males, the open triangles female A and the filled triangles the results of female B.*

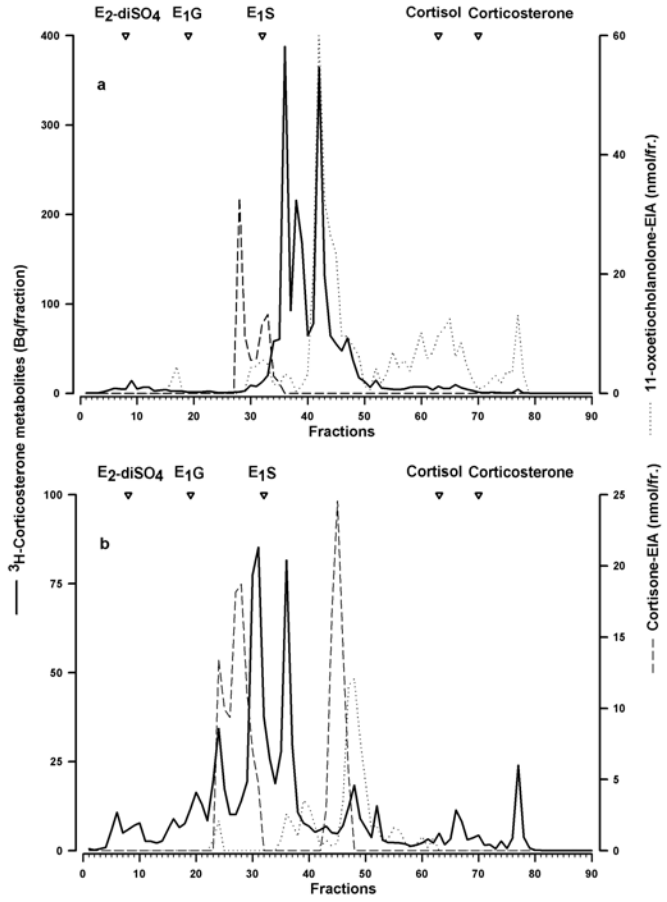

Figure 2. *RP-HPLC separation of ^{3}H-CM in droppings of (**a**) a male and (**b**) a female Capercaillie. Radioactivity of each fraction was determined by liquid scintillation counting. The immunoreactivity of ^{3}H-CM with two different EIAs is given in nmol per fraction. Open triangles mark the approximate elution position of respective standards: E_2-diSO_4 = estradiol-17β-disulphate, E_1G = estroneglucuronide, E_1S= estronesulphate, cortisol and corticosterone.*

Physiological validation

In order to assess the biological relevance of the method, ACTH was injected in 5 birds to stimulate adrenocortical activity. The cortisone assay measured the highest concentrations in the samples. After injection, the concentration of CM in the droppings increased sharply, peaked after 1 – 3 h, and returned to basal values between 4 h and 13 h after injection. The increase in CM above basal levels varied individually between a factor of about 5 up to a factor of about 60 (Fig. 3). In contrast the 11-oxoetiocholanolone-EIA detected lower concentrations and no clear response to the stimulation of the HPA-axis (data not shown).

Concentrations of CM excreted during the 28 h before injection of ACTH were regarded as basal values. Although some variation of the concentrations occurred, the pattern did not resemble a

distinct diurnal rhythm (mean ± SD of the three individuals: 212±70; 228±178; 391±192 nmol/kg dropping).

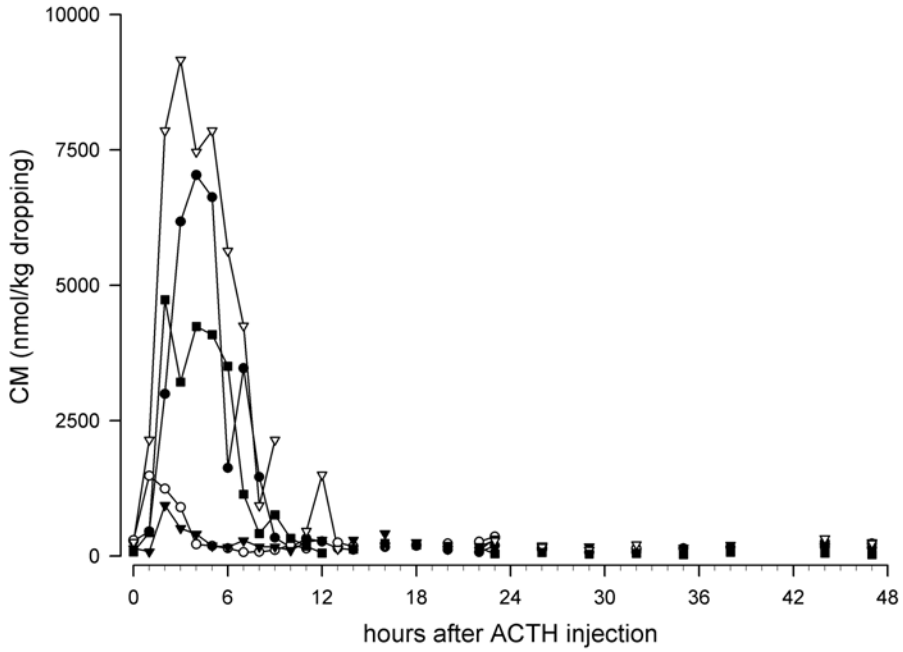

Figure 3. *Concentrations of CM (3,11-dioxo-CM, nmol/kg droppings) after administration of ACTH in droppings of 3 male and 2 female Capercaillies.*

Effects of storage

The average concentration of CM in the samples frozen within 1 day after voidance was 537 ± 79 nmol/kg for males and 339 ± 50 nmol/kg droppings for females. There were significant effects of temperature and storage time on the concentration of CM as well as of the gender*temperature, temperature*time and gender*temperature*time interactions (Table 1). The main effect of gender and the gender*time interaction were not statistically significant.

Both temperature and storage time changed the concentration of CM in the droppings compared to droppings frozen within 24 h after voidance (Fig. 4). In samples incubated at 8°C, CM were not significantly different from those in frozen samples, but in samples exposed to 21°C for 21 days concentrations were significantly higher in both genders.

Table 1.

Effect of gender, ambient temperature, and storage time on the concentration of CM in droppings.

Source of variation	d.f.	m.s.	F	P
Aviary stratum	2	0.084	0.28	
Individual per aviary stratum				
Gender	1	1.726	5.85	0.137
Residual	2	0.295	12.86	
Units per individual per aviary				
Temperature	2	0.92605	40.37	<.001
Time	3	0.39155	17.07	<.001
Gender*temperature	2	0.22437	9.78	<.001
Gender*time	3	0.02807	1.22	0.302
Temperature*time	1	0.32875	14.33	<.001
Gender*temperature*time	1	0.29662	12.93	<.001
Residual	251	0.02294		
Total	268			

Nested ANOVA with ln[CM] as dependent variable and aviary, gender, temperature, storage time and interactions as independent variable. For details of the model, see text. Units of the analysis consist of a single portion of the homogenized droppings. Abbreviations: d.f. = degrees of freedom; m.s. = mean squares; F-value and significance P are given.

Discussion

Radiometabolism study

The radiometabolism study aimed at tracking the temporal excretion pattern of CM and to select the droppings with the highest radioactivity to characterize the excreted CM. The excretion of the ^{3}H-corticosterone started immediately after injection. In three birds high concentrations of radioactivity were measured during 1 - 4 hours, appearing as one broad peak. Only in one female two peaks of ^{3}H-CM could be observed, 1 h and 3 - 4 h after injection. This biphasic excretion pattern of female B agrees with that described for domestic chicken.[28] In the chicken, the first peak could be assigned to the metabolites excreted via the urine and the second peak to the excretion of the metabolites via the feces.[28] Since, birds excrete urine and feces together via the cloaca, the two components cannot readily be separated as it is possible in mammals.[34,37,43]

The unimodal temporal excretion pattern found in the three normally excreting individuals may be explained by the particular diet and specific characteristics of digestion of Capercaillies. During winter, Capercaillies feed mainly on conifer needles (> 90%). This fibre-rich diet quickly passes through the intestine, except the nutrient-rich, liquid component, which enters the ceca. This diet is poor in water and protein[8,36], thus only little amounts of urine are excreted. Furthermore, urine is transported from the cloaca back to the ceca by reverse peristalsis for reabsorption of water.[44] Hence, urine is mixed with feces by its forth and back movement in the rectum. Consequently, the CM secreted by the kidney and the bile are mixed and excreted together, which results in a broad peak appearing relatively quickly. The fact that the single hen with the biphasic pattern excreted liquid (and therefore less mixed) droppings instead of the normal dry ones, supports this idea.

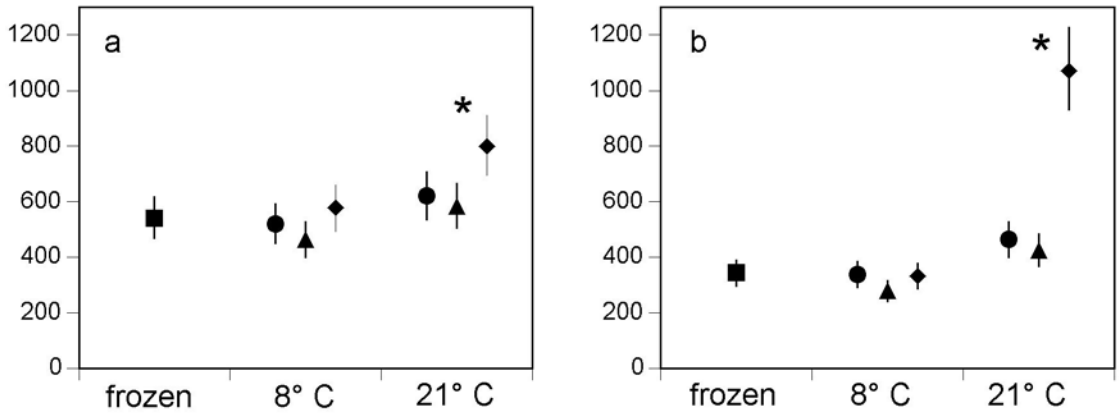

Figure 4. *Concentrations (mean ± SE; n = 15) of 3,11-dioxo-CM (nmol/kg droppings) after storage at 8°C and 21°C for 1 (circle), 7 (triangle) and 21 (rhombus) days, respectively for (**a**) males and (**b**) females. Control samples (n = 45) were frozen at –23°C within 24 hours after collection. Conditions marked with an asterisk differ significantly (P < 0.05) from control samples.*

Glucocorticoids are heavily metabolized before excretion.[34] In the RP-HPLC analysis of the droppings with the highest concentrations of radiolabeled CM, corticosterone itself could be found only in very small amounts, if at all, in the birds. This is in accordance with other studies, which also did not find any corticosterone in droppings (Black grouse *Tetrao tetrix*[39] Great tit *Parus major*[27] European stonechats *Saxicola torquata*[25] domestic chicken[28]). The RP-HPLC analysis indicated that metabolites more polar than corticosterone were excreted. Since the three to four most prominent fractions were polar, conjugated or polar unconjugated metabolites were most abundant. These results agree with those in other bird species, in which radiometabolism studies were performed (chicken, geese and black grouse), all showing mainly polar metabolites.[22,28,39]

Physiological validation

Stimulation of the hypothalamic-pituitary-adrenocortical (HPA) - axis by injection of ACTH promotes synthesis and secretion of glucocorticoids[45], which finally results in an increase of the CM in the droppings.[28] Following ACTH injection, the Capercaillies' CM concentrations increased after the first hour and peaked after about 3 - 4 hours before they slowly returned to pre-treatment levels. This agrees with the temporal pattern of excretion in the other grouse species, the Black grouse.[39] In chickens[28] and Spotted Owls *Strix occidentalis caurina*[26] peak concentrations of CM appeared already 2 h after the stimulation. The delayed excretion of peak concentrations in Tetranoids is probably due to the fact that urine is transported back from the cloaca to the ceca and therefore mixed with the feces as discussed before.

The cortisone - EIA, which detects metabolites with a 3,11-dioxo structure and the 11-oxoetiocholanolone assay, measuring CM with a 5β-3α-11-one structure showed a high immunoreactivity in the HPLC fractions. However, only the cortisone assay showed an expressed increase of concentrations following ACTH. This demonstrates the importance of a physiological validation. As this group specific antibody proved also best suited for chicken and Black Grouse[28,39] it seems to be the most adequate for the determination of the CM excreted by Galliformes.

Effects of storage

The concentration of CM in the feces can vary with storage conditions and time.[31,32] Because the exact time since voidance of Capercaillie droppings found in the field is unknown, we measured CM concentrations in droppings that were exposed for different time spans and at different temperatures. This approach may help to establish a sampling protocol suited for field conditions.

The results of the storage experiment showed that the concentration of the CM varied with gender, storage time and temperature, but only at room temperature. In both genders the concentrations increased significantly after 21 days of storage at room temperature. In comparison with the frozen samples, no significant change could be observed in droppings stored at 8°C up to 21 days. Therefore, in studies conducted in the mountains during the winter with ambient temperatures around or below the freezing point, changes in the concentration of CM after voidance will most probably be insignificant.

An increase in glucocorticoid metabolite concentrations was also observed in mammals, when feces were incubated at room temperature. These studies measured increased concentrations after an storage time of 4 h in cattle and 24 h in horses. Most probably, naturally occurring bacteria metabolize steroids with their enzymes[31,32].

Gender differences in pattern and amounts of excreted fecal CM were described for chickens.[28] Because of the various difficulties of raising and keeping Capercaillies only a small number of animals could be used in our study. Therefore statistically significant gender differences could not be proven. However gender should be taken into account when interpreting the results of studies of fecal samples. For our sampling protocol in the field this gender difference poses no problem, because the droppings of male Capercaillies from roosting trees can be distinguished from those of females by their larger size.

Diurnal pattern

The samples collected during 28 h did not reveal a diurnal rhythm. This agrees with findings in the Black Grouse[39], but is in contrast to several studies measuring plasma corticosterone levels in other birds[46,47], in which corticosterone concentration rises in the early morning, before activity starts. Grouse species during winter typically have a particular activity pattern. They feed only twice per day, in the morning and afternoon, while they roost in snow burrows, below or on trees during the rest of the day. This bimodal activity and feeding pattern is maintained in captivity. Hence, it is not surprising that their daily corticosterone pattern differs from that of other bird species kept in captivity.

As for the sampling protocol in the field, it seems that there is no need to observe time of day. However, as there are differences in corticosterone metabolite concentrations between droppings e.g.[39], possibly related to a pulsed excretion of corticosterone by the bile (Klasing, pers. commun.), several droppings from below a roost tree or a burrow should be collected and homogenized. With this, a mean concentration of CM excreted over a longer time span will be obtained.

Conclusion

This study demonstrates that the concentration of CM can be reliably measured in droppings collected from Capercaillies under field conditions during winter. CM excreted in droppings are best determined

with the cortisone – EIA (measuring 3,11-dioxo CM), as shown by the radiometabolism study and the ACTH validation experiment. Genders probably differ in the concentration of CM in droppings, but droppings can be separated according to sex in the field in most cases. Droppings should be collected within about 20 days and should be exposed to temperatures not exceeding 8°C. The maximum age of the droppings can usually be determined when observing the last snowfall and ambient temperatures exceeding 8°C are rare during winter in the habitat of the Capercaillie. Several droppings should be analysed together in order to avoid variations between droppings and to obtain a mean value over a longer time period. Hence, the method to estimate whether Capercaillies are physiologically stressed from droppings seems to be promising.

Acknowledgements

We thank Peter Berthold, Max-Planck Institute for Ornithology, Radolfzell, for permission to do the experiments with his Capercaillies, Alexandra Kuchar and Ruedi Meier for laboratory assistance, Marc Kéry for statistical advice, Niklaus Zbinden and Lukas Jenni for valuable comments.
Birds were hold and all experiments were carried out under license from the Regierungspräsidium Freiburg, G-03/21.

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Paper II

Selection of night roosts in winter by capercaillie *Tetrao urogallus* in Central Europe

In press as:

Dominik Thiel[1, 2], Christoph Unger[3], Marc Kéry, and Lukas Jenni1. Selection of night roosts in winter by capercaillie *Tetrao urogallus* in Central Europe, Wildlife Biology, in press.

[1]Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

[2]Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

[3]Institut für Ökologie, Friedrich Schiller Universität, Dornburger Strasse 159, 07743 Jena, Germany

Abstract

To survive in harsh winter conditions, animals must make behavioural and physiological adaptations. The selection of good habitats may prevent a negative energy budget and reduce predation risk. The capercaillie *Tetrao urogallus*, the largest of all grouse, feeds in winter on conifer needles, a superabundant but low-energy food resource. We hypothesized that capercaillie should select nocturnal roosting trees that simultaneously provide food, minimize predation risk and reduce energy expenditure. Using paired logistic regression, we studied night roost selection in winter in the Black Forest (Germany), the Swiss Jura, the Swiss Alps and the Thuringia Forest (Germany) by comparing 508 pairs of roosting trees and matched control trees. The most important factors discriminating roosting trees from random trees were tree species and number of forest aisles leading away from the roost tree. Trees with more than one nearby forest aisle for escape by flight were preferred over those with only one aisle or none. Capercaillie strongly selected pine trees *Pinus spp.* for nocturnal roosting, and avoided Norway spruce *Picea abies*. At sites without pine trees, deciduous trees were preferred. Compared to females, males preferred larger trees in more open forest stands. Our results suggest that the selection of night roosts is determined by predator avoidance, energy-saving strategies aimed

at reducing flight activity and feeding possibilities. Microclimate does not seem to influence selection of night roosts.

Introduction

In northern and temperate areas, winter is a challenging time for most bird species, often causing high mortality (Wegge et al. 1987, Peach et al. 1999, Bro et al. 2000). Climatic conditions are typically harsh, food availability is reduced and predation level high. Particular physiological and behavioural adaptations are required to survive under such conditions. One adaptation is the selection of a winter habitat that favours energy-saving strategies and reduces predation risk.

The capercaillie *Tetrao urogallus* is a sedentary grouse species that is listed in the national red data books of central and western European countries (Storch 2000). Capercaillie inhabit a large variety of boreal and mountainous coniferous forests in the Palaearctic, and owing to their great body mass, up to four kilograms, need large amounts of food in winter. During winter, capercaillie feed almost exclusively on conifer needles (Pulliainen 1970, Storch et al. 1991). Needles are a superabundant food resource, but are low in energy and are difficult to digest because of their high content of cellulose and secondary plant compounds (Lindén 1984, Andreev 1988). Capercaillie partly overcome these problems by selecting needles with a high energy and a low resin content (Lindén 1984, Annila et al. 2003). Cellulose is decomposed and digested with the aid of bacteria in specially adapted caeca during a long-lasting process (Moss & Hansson 1980). Because of the particular characteristics of their food and digestion, capercaillie are severely constrained in their rate of energy intake and therefore need to minimize energy expenditure to prevent a negative energy balance (Rintamäki et al. 1984, Andreev & Lindén 1994).

Therefore, optimal selection of winter habitat by capercaillie should result in a reduction of energy expenditure and predation risk, rather than in increased food availability like in many other species (Rolando & Carisio 1999). Energy expenditure can be reduced by minimizing the distance or the frequency of flights between foraging and roost sites, and by choosing favourable microclimatic conditions for roosting. Predation risk can be reduced by choosing habitats with few predators or by adapting a behaviour during foraging and roosting that enables escape flights or hiding.

Habitat requirements may differ between day and night. For example, many species such as ravens *Corvus corax* and Savannah sparrows *Passerculus sandwichensis* feed at particular sites and fly up to many kilometres to attain their roosts (Wright et al. 2003, Ginter & Desmond 2005). In the case of the capercaillie, such flights should be kept to a minimum to minimize energy expenditure and predation risk. Capercaillie roost in both trees and in snow burrows, burrows being used mainly by more northern populations (Seiskari 1962). In the populations that we studied, birds roosted only in trees and therefore it would be advantageous if day and night tree roosts were close together or even in the foraging trees. However, to our knowledge, characteristics of night roosts have not been analysed in capercaillie.

In our study, we examined the following four hypotheses: (1) Capercaillie should choose night roosts to save energy by minimizing the distance of flight between trees used for foraging and night roosts. Furthermore, capercaillie should select favourable microclimatic conditions with wind protection to reduce heat loss at exposed roosts (Walsberg 1986). Therefore, we would expect

capercaillie to roost in dense stands of conifers offering food and a favourable microclimate. (2) Night roosts should be inaccessible to most predators, offer escape routes and enable capercaillie to detect approaching predators. Therefore, we would expect night roosts in trees rather than on the ground, to avoid red foxes *Vulpes vulpes*, an abundant predator in Central Europe (Storch et al. 2005). For protection against predators that climb trees (e.g. martens, *Martes spp.*), we would expect capercaillie to select open forest stands that allow the detection of approaching predators and that also offer forest aisles or proximity to forest edges for escape flights. (3) These two hypotheses are in conflict, because the minimization of energy expenditure requires dense stands with a favourable microclimate (Thompson & Fritzell 1988) whereas the detection of predators requires open stands of trees. Therefore, we would expect capercaillie to favour pine trees *Pinus spp.* whenever available, because they offer the preferred needle forage (Lieser et al. 2005), and usually grow in relatively open forest stands enabling predator detection and escape flights. In areas without pines, capercaillie should roost in other relatively open conifer stands. To investigate this hypothesis, we examined roosting sites in two study sites with pines and two sites without. (4) Energy expenditure, predation risk and escape behaviour vary between the sexes because body mass of males is nearly twice that of females. We predict that, compared with females, the larger males with their lower mass-specific energy requirements and heat loss, and their much lower critical temperature (Rintamäki et al. 1984) should choose night roosts with a less favourable microclimate. In addition, males should prefer larger roosting trees in forest stands with more space for escape flight.

Methods

Study sites

The study was carried out during the winters (November to March) of 2003–2004 and 2004–2005 in four different study sites in Central Europe (Fig. 1): in Southern Black Forest, Germany (47°51'N, 8 °00'E), Western Swiss Jura (46°33'N, 6 °15'E), Swiss Alps (46°45'N, 9 °04'E) and Thuringia Forest, Germany (50°30'N, 11°08'E). In the Black Forest study site (11 km^2), elevations ranged between 1,000 and 1,400 m a.s.l., and forests are intensively used for forestry and tourism. Forests were dominated by dense nutrient-rich forest stands containing Norway spruce *Picea abies* (49%) and European silver fir *Abies alba* (19%; Suchant *et al.* 2003). Common beech *Fagus sylvatica* (22%) was the most abundant deciduous tree. The study site in the Western Swiss Jura (4 km^2) encompassed forests ranging between 1,300 and 1,500 m a.s.l. and dominated by Norway spruce (73%) mixed with common beech (10%), sycamore maple *Acer pseudoplatanus* (4%) and European silver fir (12%; U. Ulmer, unpubl. data). Pines were absent in the Black Forest site and in the Western Swiss Jura. The study site in the Swiss Alps consisted of 36 independent plots ranging from 14–200 ha, with a mean size of 89 ha, and totalling 32 km^2. The plots consisted of a large variety of different forest types, forest sizes, forest management regimes and altitudes ranging from 1,300 to 2,200 m a.s.l. Tree composition varied from pure to mixed coniferous forests with different tree species dominating (*Pinus mugo*, *Picea abies*, *Pinus cembra*, *Larix decidua* or *Abies alba*). Deciduous trees were absent from nearly all the Swiss Alp plots. Tree composition in the dense productive Thuringia Forest, with a prospected area of about 70 km^2 and elevations between 600 and 850 m a.s.l., was dominated by

Norway spruce (>80%), with only small proportions of other species (*Pinus sylvestris* 5–10%, *Fagus sylvatica* <1%) present. All four forests were subjected to forest management and tourism.

Estimated population size in the Black Forest study site is over 60 capercaillie (Braunisch & Suchant 2006), about 56 in the Swiss Jura study site (S. Sachot, pers. comm.), at least 290 in all Swiss Alp plots combined (K. Bollmann and P. Mollet, pers. comm.), and about 25 in the Thuringia Forest (S. Klaus, pers. comm.). These numbers probably underestimate the number of individuals for which we sampled roosting trees, because we sampled data over two years and because the reproductive success of capercaillie in 2003 increased population to levels higher than the figures stated above.

During the study, snow covered the ground vegetation completely in all study sites. Snow depth ranged from 10 cm in the Swiss Jura in early winter to at least 200 cm in late winter in the Black Forest and in the Swiss Alps. The top layer of the snow cover varied. It was a hard frozen crust when temperatures were above 0°C at daytime and below 0°C at night. After fresh snow falls with temperatures far below 0°C, the snow was loose and dry. In all study sites, daily mean temperatures between November and March in the winter 2004–2005 (measured 2 m above ground) were <0°C.

Data collection

In all four study sites, night roosts were found by walking along contour lines crossing forests within mapped capercaillie areas, and by visually searching for faeces on the snow surface. The probability of detecting a capercaillie snow roost is probably lower than that of finding a night roost in a tree. However, during our studies we found several snow burrows of hazel grouse *Bonasa bonsasia* and black grouse *Tetrao tetrix*, but none of capercaillie. Therefore we believe that snow burrows of capercaillie were rare, but possible to detect. Each forest was visited once in early winter (November–December) and once in late winter (February–March). In addition, in the Black Forest and Thuringia Forest sites, we also found several night roosts while tracking radio-equipped capercaillie. Our data may contain a certain amount of pseudo-replication, because forests were visited twice. However, the number of capercaillie in the Swiss Alps and in the Black Forest study site was quite high, thus reducing pseudo-replication.

The conspicuous faeces on snow under night roost trees make them easy to detect. Night roosts were distinguished from day roosts by the presence of both caecal faeces and a concentrated heap of long, cylindrical intestinal faeces. Because capercaillie excrete one intestinal faeces every 12 minutes (Klaus et al. 1989), and night roosts are used from dusk to dawn in winter, large heaps of intestinal faeces are a distinct characteristic of a night roost. For each roosting tree located, we chose one currently unoccupied control tree by walking 50 m from the night roost in a random direction. The tree closest to this point and with a circumference at breast-height of at least 20 cm was selected as the control tree. From past experience, we knew that capercaillie always roosted on trees with a circumference > 20 cm, and this was confirmed by the present study. In total, we analysed 508 pairs of trees.

We investigated predictor variables known to be important for capercaillie winter habitat selection (Klaus et al. 1989, Storch 1993a). To test our hypotheses, we selected variables that could vary within the investigated spatial scale of the tree pairs, and which characterize the appearance of

forest stands as perceived by a capercaillie sitting in a tree. For each roost and control tree, we recorded study site (SITE; Black Forest, Swiss Alps, Swiss Jura, Thuringia Forest), circumference at breast-height of the tree (CBH), and tree species (TREESPEC; *Picea abies*, *Abies alba*, *Pinus* spp., *Larix deciduas,* deciduous tree). Pine trees included *Pinus cembra, Pinus mugo* and *Pinus sylvestris*. Within a 20-m radius of the trees, we estimated canopy cover as the vertical projection on the forest floor (CANOPY; in %), and recorded forest aisles (AISLE; none, 1, >1), and steepness of the slope (SLOPE; in °). A forest aisle was defined as a canopy opening at least 5 m wide and 20 m long leading away from the roost or control tree. In addition, we measured the distance to the nearest edge (EDGE; forest edge, habitat edge or other disrupting element such as a forest road).

For 61 pairs of roost and control trees in the Black Forest in winter 2003–2004, we recorded CBH and species of all trees within a radius of 20 m (1,257 m^2). Based on these measurements, we computed the deciduous and the conifer tree stocking values (Bickford 1957) by establishing the sum of the cross-section areas of all stems at breast-height. Because the two values for deciduous and conifer tree stocking were highly negatively correlated, only the deciduous tree stocking (DTS) was used in the analysis.

For all night roosts, we determined the sex of the capercaillie from the size of the intestinal faeces, i.e. faeces diameter of males >10 mm, and those of females <8 mm (K. Bollmann, unpubl. data). Determination of sex of capercaillie in winter from the size of nocturnal faeces is a reliable method (Gjerde 1990), because faeces do not swell in ambient temperatures below 0°C, and are of comparable consistency due to the unique food source of conifer needles. Night roosts with faeces in the overlapping zone of 8–10 mm were excluded from sampling (~12). We recorded the position of the bird in the tree by measuring the distance between the tree trunk and the centre of the faeces. We noted the orientation of the roosting branch relative to the slope (downhill, uphill, sidewards, or flat for trees in non-sloping forest stands).

Statistical analyses

We used a matched-pairs (also called paired) logistic regression analysis to identify factors related to the choice of roosting trees in capercaillie. In studies of rare events, such as the use of a tree for roosting by a capercaillie, the only realistic sampling design may be to take a sample of roosting trees (cases) and compare each roosting tree to a nearby matched unused (control) tree. In this situation, standard logistic regression is inappropriate and instead paired logistic regression should be used to analyse the determinants of the rare event (Hosmer & Lemeshow 1989, Keating & Cherry 2004). Paired logistic regression is more powerful, since it exploits the information about the pairing of cases and controls, but seems to have been discovered only recently by biologists (see examples in Rocke & Samuel 1999, Weller & Zabel 2001, Compton et al. 2002).The parameter estimates of the paired logistic regression model are interpreted in terms of the relative risk (odds ratio) of the event, i.e., a tree being used for roosting. The procedure is similar to a paired t-test, where the difference between each pair is a single observation.

To test which tree and habitat variables were most important in distinguishing roosting trees from non-roosting trees, we conducted two different paired logistic regression analyses. In analysis A, we included data from all 508 tree pairs from all four study sites (129 tree pairs in the Black Forest,

213 in the Swiss Alps, 46 in the Swiss Jura, and 120 in the Thuringia Forest), and six explanatory variables without the variable SITE. To test for differences in the preference of tree and habitat characteristics between sites, we included eight biologically relevant interaction terms. Obviously, there is no main effect of SITE, since in our paired design, both trees of a pair always shared the same SITE. Instead, effects of SITE are tested in interaction terms with the other explanatory variables CBH, CANOPY, EDGE, SLOPE and AISLE. The interaction between SITE and TREESPEC could not be included in the model, since some tree species did not occur in all sites. This produced empty cells in the design matrix of the model and prevented computation (see Hosmer & Lemeshow 1989). Furthermore, we included the interactions between AISLE and EDGE and CANOPY, respectively, as well as between EDGE and CANOPY, because we expected them to be biologically relevant. Exploratory analysis showed that no substantial correlation of two continuous predictor variables for roosting trees existed (R^2<0.10).

Analysis B was similar to analysis A but applied to the data from the 61 tree pairs in the Black Forest, where the additional explanatory variable deciduous tree stocking DTS had been recorded. Obviously, SITE and all interactions with SITE were not included in the analyses, because all trees were in the Black Forest. Because of the small sample size and the absence of pine and larch trees, the TREESPEC factor was reduced to two levels (conifer trees and deciduous trees), and no interaction effects were tested.

In analysis C, we tested for sex differences in the use of 508 night roosting trees, 312 trees being used by males and 196 by females. We applied standard logistic regression analysis to compare sex differences, rather than discriminant function analysis, because it permits inclusion of categorical predictors (North & Reynolds 1996). The response variable was set at 1 for males and 0 for females. The explanatory variable AISLE had only two levels, because there were no cases of hens using trees with no forest aisles. Therefore, we lumped “no” and ”one” forest aisle into category 1 and “> 1” forest aisle into category 2. In contrast to analyses A and B, standard logistic regression analysis could be used to test the effects of the main factor SITE and its interaction with TREESPEC.

Akaike’s Information Criterion AIC (Akaike 1974) was used to select the best model for all three analyses A, B and C. First, we developed a list of candidate models *a priori* based on our hypotheses. For analysis A, this list included 14 candidate models, including the range from the simplest model, with one main effect, to the most complex model with six main effects (without SITE) and eight interaction terms. For analysis B, seven candidate models were built, including the range from the simplest model with one main effect, to the largest model with all seven main effects without any interaction terms. The list for analysis C contained 15 candidate models including the range from the simplest model with one main effect, to the most complex model with all seven main effects and eight interaction terms. Secondly, models within each analyses A–C were ranked using AICc (Hurvich & Tsai 1989), and the final model of each of the three analyses A–C with the minimum AICc was selected to fit to the data. We used GenStat for Windows version 7.3 (Payne 2003) for all analyses.

Results

Nocturnal roosting tree selection

All night roosts were in trees. In 188 out of 508 cases, roosting trees were in flat forest stands (< 5° slope). In sloping forest stands, capercaillie mostly roosted on tree branches, which pointed downhill (50% for males, 43% for females), followed by branches pointing uphill (31% for males, 44% for females), and sidewards (19% for males, 14% for females); differences between sexes were not significant ($\chi^2 = 5.34$, df = 2, P = 0.07). Birds roosted at a mean distance of 171 cm (SE ± 6 cm, N = 501, range = 15–560 cm) from the trunk. There was no significant difference between sexes (ANOVA, df = 500, F = 1.36, P = 0.24).

In analysis A, the best model selected by AICc was the second most complex model containing all six main effects and seven interaction terms (Table 1). The second best model included one more interaction term. All other models had negligible support. The selection of the two most complex models is probably caused by the fact that study site (SITE) is not included as a main effect, but rather as an interaction term. This indicates that all our variables, and especially the predictor variable SITE, made an important contribution to the model. According to the odds ratios of the main effects and the interaction terms, roosting trees differed from randomly chosen paired control trees mainly by tree species and the presence of flight aisles (Table 2). The effect of the latter mainly depends on the study site (see large odds ratios of the interaction terms SITES*AISLE in Table 2). Independent of the study site, Norway spruce was always avoided for nocturnal roosting, and the preferred trees were deciduous species (*Fagus sylvatica* and *Acer pseudoplatanus*), pines, silver fir and larch (Table 2). Many night roosts were in pines (45%), whereas the most common control tree was Norway spruce (67%). In the study sites Black Forest and Swiss Jura without pines, deciduous trees were strongly preferred for nocturnal roosting. In the Swiss Alps and in the Thuringia Forest without deciduous trees (Fig. 2), pines were strongly preferred for night roosts.

Also tree size (CBH), canopy cover, edge distance and slope contributed to roosting tree selection. Roosting trees had larger stem circumferences (CBH) than control trees, by 15 cm on average (Fig. 3a). Only in the Black Forest was stem circumference of roosting trees slightly smaller than in control trees (Fig. 3a). The difference in the CBH medians between roost and control trees for Norway spruce was 13 cm. The corresponding difference for deciduous trees was 23 cm, 30 cm for silver fir, 21 cm for pines, and 29 cm for larch trees. Canopy cover around roosting trees was less than around control trees at two study sites (Fig. 3b). In all sites, trees with more than one forest aisle were highly preferred for nocturnal roosting, and those with no or one forest aisle were avoided (Fig. 4, Table 2). The large odds ratios and errors of the interaction terms of SITE3 and SITE4 with AISLE2 (one flight aisle) are due to the fact, that in the Swiss Jura and in the Thuringia Forest, roosting trees with one flight aisle were highly selected compared to those with no flight aisle (AISLE1 is set to zero), because there were no roosting trees with no flight aisle (Table 2). Roosting trees were usually closer to a forest edge than control trees (Fig. 3c). The effects of canopy cover and edge distance differed by site (Table 2, Figures Fig. 3b and 3c). Roosting trees in the Black Forest and in the Thuringia Forest were closer to edges and had a less canopy cover in the surroundings than control trees. In the Swiss Alps, the opposite was found. In the Swiss Jura, distance to forest edge did not differ between roost and control trees, but canopy cover was 10% higher around roosting trees than around control trees

(Fig. 3b). The largest odds ratio among the first four interaction terms (AISLE*CANOPY) indicates that the importance of canopy cover in the surroundings differed according to the presence of forest aisles. The median canopy cover around roosting trees without forest aisle was 45% vs. 70% for control trees without forest aisle. The canopy cover for roosting trees with one forest aisle was 45% vs. 48% for control trees. For roosting trees with more than one forest aisle, canopy cover was 32% vs. 25% for control trees.

In analysis B, we investigated 61 Black Forest tree pairs and measured the tree-stocking value in the circular areas surrounding each tree. AICc clearly selected the model including all possible predictor variables, including the deciduous tree-stocking DTS (Table 3). According to the large odds ratios of the variables TREESPEC and AISLE>1, roosting trees differed from randomly chosen paired control trees mainly by tree species and the presence of flight aisles (Table 4). Trees offering more than one forest aisle were highly preferred for nocturnal roosting, whereas control trees had usually no or just one forest aisle. Deciduous trees were highly preferred for nocturnal roosting, whereas conifer trees were avoided. Sixty-four percent of all roosting trees were deciduous, while only 21% of the control trees were deciduous. Forest stands around roosting trees had a significantly higher deciduous tree stocking value (median = 0.74 m^2, range = 0–3.89 m^2) than those around control trees (median = 0.36 m^2, range = 0–2.79 m^2).

Sex differences in nocturnal roosting tree use

In analysis C, coefficients of the three best models selected by AICc with combined model weights of 0.93 suggest that tree selection for night roosting differed significantly between the sexes for all predictor variables (Tables 5 and 6). The second and third best models also included one and two interaction terms respectively. Males usually preferred trees with a greater stem size (CBH) than females did (Fig. 5a). Compared to females, males preferred forest stands with a less canopy cover (Fig. 5b), situated in less sloped forest stands and closer to forest edges. In the two sites with pines (Swiss Alps and Thuringia Forest), males roosted in pines more often than females did (Fig. 6). In the two sites without pines (Black Forest and Swiss Jura), females roosted more frequently in deciduous trees than in other tree species (Fig. 6).

Discussion

Capercaillie showed a strong preference for certain tree and forest characteristics for nocturnal roosting in winter. Pines or deciduous trees with more than one forest aisle were strongly preferred for nocturnal roosting, and spruce trees with no forest aisle were avoided. Furthermore, the birds preferred large trees (CBH) in open forest stands close to forest edges, and avoided small trees in relatively dense forest stands. Compared to females, males favoured larger trees in more open stands, closer to forest edges and on gentler slopes.

Night roost selection according to energetic aspects

According to our first hypothesis, capercaillie should roost on the preferred feeding trees to avoid energy-consuming flights. Indeed, if pines were present (Swiss Alps and Thuringia Forest), pines were the most often used trees for night roosting. Several studies have confirmed that capercaillie prefer

pine needles to other needles for feeding (Glutz von Blotzheim et al. 1973, Schroth et al. 2005). In both sexes, habitat selection in winter is mainly determined by the presence of pines for feeding and roosting (Gjerde 1991), and spruce-dominated stands are avoided (Gjerde & Wegge 1989). Lindén (1981) pointed out that pine forests are the most common winter habitat for capercaillie in Finland because the combined availability of food and shelter enable the birds to minimize the duration of their activity periods. Therefore, foraging, diurnal roosting and nocturnal roosting can all be done in the same tree or within the same pine forest stand without energy-consuming flights to change trees. Although this has not been investigated with radio-tracking studies, other results point in the same direction, supporting the hypotheses of energy saving and predator avoidance. For example, home ranges are smaller in winter than in summer (Storch 1995), the daily activity period in winter lasts only 2–3 hours (Gjerde & Wegge 1987), and capercaillie confine their movements to small core areas within individual winter home ranges (Gjerde et al. 1985).

Contrary to our first hypothesis, microclimatic conditions did not determine night roost selection in our study sites, although temperatures during most nights were below the thermo-neutral zone of capercaillie, as the lower critical temperature is at –3°C for males and +9°C for females (Rintamäki 1984). Two of our results point in this direction. First, even when snow and temperature conditions were favourable for snow roosts, we did not find any. This is in contrast to northern and boreal capercaillie populations, where capercaillie often roost in snow burrows (Lindén 1981, Klaus et al. 1989), and benefit from higher temperatures within snow roosts (Marjakangas et al. 1984). Snow roosts seem to be used rarely by capercaillie in Central Europe (Catusse 1989). Secondly, the windy deciduous trees were highly preferred for nocturnal roosting at sites without pines. Norway spruce was avoided although their dense forest stands and much canopy cover provided protection against harsh weather conditions. In the few cases where capercaillie used Norway spruce for roosting, they selected trees with few or no branches below the roosting branch. The preference for open roosting trees in capercaillie is in contrast to studies on winter night roosts of blue grouse *Dendragapus obscurus* (Pekins et al. 1991), hazel grouse (Swenson & Olsson 1991) and ruffed grouse *Bonasa umbellus* (Thompson & Fritzell 1988). Ruffed grouse avoided deciduous trees, hazel grouse preferred to roost in Norway spruce, and all three species preferred dense conifer trees or forest stands with much canopy cover for nocturnal roosting. The authors interpret these findings with respect to thermal benefits, reduced heat loss and concealment from predators.

Night roosts selection and predator avoidance

Several of our findings indicate that predator avoidance and the availability of escape flight routes strongly influenced night roost selection, which agrees with our second hypothesis. First, capercaillie in our study never used snow roosts even when snow conditions would have allowed it. The high densities of red foxes may explain this pattern. Fox densities in Central Europe are much higher than in more northern and boreal areas such as Scandinavia (Kauhala et al. 2006), where snow roosting of grouse is mainly explained by microclimatic advantages and predator avoidance (Marjakangas 1990). Secondly, the preferred characteristics of roosting trees were open crowns growing close to forest edges in stands with a little canopy cover and with more than one forest aisle available for escape. The highly selected pines grow in open forest stands. Moreover, crowns of pines are less dense than

those of spruce trees, which were avoided. Such open forest and open tree structure facilitate both detection of predators and escape flights. Due to the capercaillie's large wingspan of up to 1.2 meters (Klaus et al. 1989), flights in many forest stands are restricted to aisles. Interestingly, trees with no forest aisles were used only when these trees were in stands with little canopy cover. The preference for branches pointing down-slope supports the importance of good escape possibilities.

In Scandinavia, major predators of adult capercaillie are goshawks *Accipiter gentilis* and red foxes (Wegge et al. 1987, Gjerde & Wegge 1989). In our study, neither of these predators can be an important threat for capercaillie roosting in trees at night, because foxes hunt on the ground and goshawks and large raptors such as the Golden eagle *Aquila chrysaetos* are diurnal. The nocturnal eagle owl *Bubo bubo* is rare or absent. Other studies confirm that martens are major predators of capercaillie (Schroth 1991, Kurki et al. 1997). Stone martens *Martes foina* and pine martens *M. martes* readily climb trees, are abundant in our study sites and hunt mainly during the night. Martens also travel through forests by jumping between crowns, but preferred roosting sites, such as solitary trees or pines in open stands, are usually isolated enough to prevent this means of access to capercaillie.

Predator avoidance patterns apparently change between day and night. Whereas capercaillie attempt to minimize predation risk at night by selecting open tree and forest structures, the opposite has been found in other studies for diurnal roosts. In Scandinavia, capercaillie selected daytime roosting sites on the ground underneath low branches with good cover at the expense of a good overview (Finne et al. 2000). Similar observations have been made in the Swiss Alps, where capercaillie shifted their daytime roosting sites from tree crowns in early winter to the ground in late winter (Bollmann et al. 2005). Therefore, a good strategy for predator avoidance during the day seems to be that of hiding in dense structures with the risk of being killed once detected. At night, the best strategy to reduce predation risk seems to include early detection of predators.

Conflict between predator avoidance and energy saving strategies

In sites without pines, capercaillie cannot simultaneously fulfil the requirements of foraging, predator avoidance and energy saving by roosting in a single tree. In such sites, capercaillie must change trees. This was the case in our study sites in the Black Forest and the Swiss Jura, where capercaillie preferred deciduous trees for roosting despite the thermal disadvantages (Walsberg 1986). In the Black Forest the deciduous tree stocking value around used trees was more than twice as high as that for control trees. In the Southern Black Forest without pines, capercaillie mainly feed on Norway spruce (Lieser 1996). Therefore, the birds must change between foraging and night roosting trees and usually between forest stands varying in tree species composition. The selection of deciduous trees as night roosts in the Black Forest can only be understood in terms of the high priority given to predator detection and escape possibilities. Forests in the Black Forest are mainly dominated by dense Norway spruce stands, and are often cultivated in plantations, thus with much canopy cover and no forest aisles or open forest structures. Deciduous trees within spruce stands often are the only sites with forest openings. Interestingly, most roosting trees were close to edges only in the Black Forest and in the Thuringia Forest, which were characterized by dense spruce stands and much canopy cover. Furthermore, only in these forests was the canopy cover of stands surrounding roosting

trees less than the cover of control trees. In the Swiss Alps and in the Swiss Jura, where the corresponding values were similar between roost and control trees, or even inverse, forests were generally more open.

Sex differences of night roost selection

In accordance with our fourth hypothesis, males preferred slightly larger trees for roosting than females. This pattern can be explained by the pronounced sex dimorphism. The larger males require larger trees with stronger branches. Males also preferred forest stands with less canopy cover. Males with their larger wingspan require more space between trees and a certain width of forest openings to fly through.

Conclusions

Night roost selection by capercaillie is part of a specific temporal and spatial habitat selection. By choosing a specific night roost, capercaillie can reduce predation risk and energy expenditure. The differences in roost sites between day and night, between northern and central Europe, and between sites with and without pines, demonstrate that capercaillie are flexible and optimize their roost sites with regard to foraging, predator avoidance and microclimate. Furthermore, the open forest structure preferred for winter night roosts agrees with the requirement that optimal summer habitats should offer forest openings with a well-developed field layer containing much bilberry *Vaccinium myrtillus* (Storch 1993b). Therefore, forest management practices that favour bilberry also favour ideal winter roosting trees with low predation risk.

Acknowledgements

We thank Dölf Egenter, Samuel Ehrenbold, Ruedi Meier, Peter Nyffeler, Emmanuel Rey, Tobias Roth, Thomas Sattler, Conny Thiel-Egenter and Thomas Wicky for their field assistance. We are especially grateful to the foresters Wolfgang Ebser and Wolfgang Röhmer-Litzmann for encouraging this study in the Black Forest. Christoph Unger thanks Siegfried Klaus for his kind support as a supervisor. For their helpful comments to this manuscript, we thank Penelope Barnett, Kurt Bollmann, Laurence N. Ellison, Susanne Jenni-Eiermann, Christian Marti, Ruedi Meier, Gernot Segelbacher, Niklaus Zbinden and three anonymous referees. Dominik Thiel received financial support from the International Council for Game and Wildlife Conservation CIC and the Janggen-Pöhn-Foundation, Switzerland. Christoph Unger received grants from the “Stifterverband für die Deutsche Wissenschaft“ and the “Stiftung Naturschutz Thüringen“.

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***Table 1**. Model selection results (Analysis A) of paired logistic regression models for night roost selection of capercaillie showing the Log-Likelihood function (Log L), number of estimated parameters (K), appropriate selection criterion (AICc), simple differences (Δ AICc), and Akaike weights (ωi). cbh= circumference at breast-height of the tree, ca=CANOPY, ai=AISLE, e=EDGE, sl=SLOPE, t=TREESPEC, si=SITE.*

Model	Variables	Log L	K	AICc	Δ AICc	ωi
1	**cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si+si*ai+e*ai+ca*si**	**185.22**	**32.00**	**-302.00**	**0.00**	**0.80**
2	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si+si*ai+e*ai+ca*si+sl*si	187.30	35.00	-299.27	2.73	0.20
3	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si+si*ai+e*si	162.43	29.00	-263.22	38.78	0.00
4	cbh+ca+ai+e+sl+t+e*ai+ca*ai	123.82	16.00	-214.53	87.47	0.00
5	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca	123.82	17.00	-212.39	89.61	0.00
6	cbh+ca+ai+e+sl+t	117.39	12.00	-210.15	91.85	0.00
7	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si+si*ai	132.09	26.00	-209.27	92.73	0.00
8	cbh+ca+ai+e+sl+t+e*ai+ca*ai+e*ca+cbh*si	124.63	20.00	-207.54	94.45	0.00
9	cbh+ca+ai+e+sl+t+e*ai	118.18	14.00	-207.52	94.48	0.00
10	cbh+ca+ai+e	13.34	7.00	-12.46	289.53	0.00
11	cbh+ca+ai+e+sl	13.87	8.00	-11.46	290.54	0.00
12	cbh+ca+ai	5.56	6.00	1.05	303.05	0.00
13	cbh+ca	-44.81	4.00	97.69	399.69	0.00
14	cbh	-66.49	3.00	139.02	441.02	0.00

Table 2. *Results of the paired logistic regression (analysis A), comparing characteristics of 508 roost trees with 508 paired control trees (see methods for details). Because tree pairs were from the same sites, SITE was not included as a main factor, but as interaction terms. The first category of categorical variables is set to zero and is not shown (AISLE_no, and Norway spruce in the category TREESPEC). SITE1 = Black Forest, SITE2 = Swiss Alps, SITE3 = Swiss Jura, SITE4 = Thuringia Forest. df = 1 for all variables and interaction terms.*

Variable	Mean deviance	Parameter estimate	Odds ratio	SE
Main factors				
DBH	44.04	0.02	1.02	0.01
CANOPY	54.50	-0.08	0.92	0.05
AISLE_one	13.65	-3.88	0.02	2.53
AISLE_several	95.31	-1.72	0.18	2.65
EDGE	14.79	-0.03	0.97	0.03
SLOPE	1.18	-0.01	0.99	0.02
TREESPEC_deciduous	70.51	3.69	40	0.74
TREESPEC_silverfir	26.11	2.04	7.71	0.56
TREESPEC_pine	45.00	2.81	17	0.54
TREESPEC_larch	18.84	3.39	30	0.83
Interaction terms				
AISLE_one*EDGE	0.58	0.02	1.02	0.02
AISLE_several*EDGE	1.03	0.03	1.03	0.02
AISLE_one*CANOPY	0.71	0.06	1.06	0.04
AISLE_several*CANOPY	5.71	0.06	1.07	0.04
CANOPY*EDGE	0.16	0.00	1.00	0.00
SITE2*DBH	0.45	0.00	1.00	0.01
SITE3*DBH	0.33	-0.01	0.99	0.02
SITE4*DBH	0.35	0.00	1.00	0.03
SITE2*AISLE2	1.92	1.21	3.35	1.59
SITE3*AISLE2	0.81	5.00	148	101
SITE4*AISLE2	4.73	6.70	812	11
SITE2*AISLE3	0.60	-0.35	0.70	1.76
SITE3*AISLE3	0.00	6.00	403	101
SITE4*AISLE3	0.99	4.50	90	11
SITE2*EDGE	2.45	-0.02	0.98	0.01
SITE3*EDGE	6.43	0.01	1.01	0.02
SITE4*EDGE	24.70	-0.09	0.92	0.03
SITE2*CANOPY	8.45	0.07	1.08	0.03
SITE3*CANOPY	5.75	0.14	1.15	0.09
SITE4*CANOPY	9.04	-0.22	0.80	0.09
SITE2*SLOPE	0.97	0.05	1.06	0.04
SITE3*SLOPE	1.06	0.08	1.08	0.08
SITE4*SLOPE	0.06	-0.04	0.96	0.18

Table 3. *Model selection results (Analysis B) of paired logistic regression models for night roost selection of capercaillie showing the Log-Likelihood function (Log L), number of estimated parameters (K), appropriate selection criterion (AICc), simple differences (Δ AICc), and Akaike weights (ωi). cbh= circumference at breast-height of the tree, ca=CANOPY, ai=AISLE, e=EDGE, sl=SLOPE, t=TREESPEC, dts=deciduous tree stocking.*

Model	Variables	Log L	K	AICc	Δ AICc	ωi
1	**cbh+ca+ai+e+sl+t+dts**	**30.42**	**10.00**	**-36.44**	**0.00**	**0.88**
2	cbh+ca+ai+e+sl+t	26.96	9.00	-32.40	4.04	0.12
3	cbh+ca+ai	11.53	6.00	-9.50	26.94	0.00
4	cbh+ca+ai+e+sl	13.33	8.00	-7.89	28.54	0.00
5	cbh+ca+ai+e	11.90	7.00	-7.68	28.76	0.00
6	cbh+ca	-3.89	4.00	16.50	52.93	0.00
7	cbh	-9.83	3.00	26.08	62.52	0.00

Table 4. *Results of the paired logistic regression (analysis B), comparing characteristics of 61 roost trees with 61paired control trees in the Black Forest (see methods for details). The first category of categorical variables is set to zero and is not shown (AISLE_no and conifer trees in the category TREESPEC). df = 1 for all variables.*

Variable	Mean deviance	Parameter estimate	Odds ratio	SE
DBH	0.37	0.07	1.07	0.04
CANOPY	14.90	-0.08	0.92	0.06
AISLE_one	6.05	0.20	1.22	1.08
AISLE>1	21.49	5.70	299	2.93
EDGE	0.50	0.02	1.02	0.03
SLOPE	1.86	-0.17	0.84	0.10
TREESPEC	14.20	9.42	12333	4.36
DTS	2.71	-0.03	0.97	0.02

Table 5. *Model selection results (Analysis C) of logistic regression models for night roost selection (n=508) differences between capercaillie males and females showing the Log-Likelihood function (Log L), number of estimated parameters (K), appropriate selection criterion (AICc), simple differences (Δ AICc), and Akaike weights (ωi). cbh= circumference at breast-height of the tree, ca=CANOPY, ai=AISLE, e=EDGE, sl=SLOPE, t=TREESPEC, si=SITE.*

Model	Variables	Log L	K	AICc	Δ AICc	ωi
1	**cbh+ca+ai+e+sl+t+si**	**-37.58**	**14.00**	**104.01**	**0.00**	**0.61**
2	cbh+ca+ai+e+sl+t+si+e*ai	-37.58	15.00	106.13	2.12	0.21
3	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai	-37.15	16.00	107.40	3.39	0.11
4	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e	-37.15	17.00	109.54	5.53	0.04
5	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh+si*ai+si*e+si*ca+si*sl	-21.10	32.00	110.64	6.64	0.02
6	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh	-35.85	20.00	113.42	9.41	0.01
7	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh+si*ai	-34.98	23.00	118.24	14.23	0.00
8	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh+si*ai+si*e	-31.91	26.00	118.74	14.73	0.00
9	cbh+ca+ai+e+sl+t+si+e*ai+ca*ai+ca*e+si*cbh+si*ai+si*e+si*ca	-29.69	29.00	121.03	17.02	0.00
10	cbh+ca+ai+e+sl+t	-51.02	11.00	124.56	20.56	0.00
11	cbh+ca+ai+e+sl	-65.72	7.00	145.66	41.65	0.00
12	cbh	-70.31	3.00	146.66	42.65	0.00
13	cbh+ca	-70.31	4.00	148.69	44.68	0.00
14	cbh+ca+ai+e	-68.40	6.00	148.97	44.97	0.00
15	cbh+ca+ai	-69.93	5.00	149.97	45.97	0.00

Table 6. *Results of the non-paired logistic regression (analysis C), comparing characteristics of 312 trees used by males and 196 trees used by females for nocturnal roosting (see methods for details). The first category of categorical variables is not shown (AISLE_no/one, Norway Spruce in the category TREESPEC, and Black Forest in the category SITE).*

Variable	DF	Deviance	Mean deviance	Parameter estimates	SE
CBH	1	7.73	7.73	0.99	0.68
CANOPY	1	0.09	0.09	0.01	0.00
AISLE>1	1	0.98	0.98	-0.04	0.01
EDGE	1	3.79	3.79	-0.63	0.30
SLOPE	1	6.80	6.80	0.00	0.00
TREESPEC	4	37.20	9.30	-0.01	0.01
SITE	3	31.80	10.60		

Figure 1. *The location of the four study sites in Central Europe where we studied night roost selection of capercaillie during 2003–2005 (© Institute of Cartography ETH Zürich). The 36 study plots within the study site "Swiss Alps" are within the frame and not shown individually.*

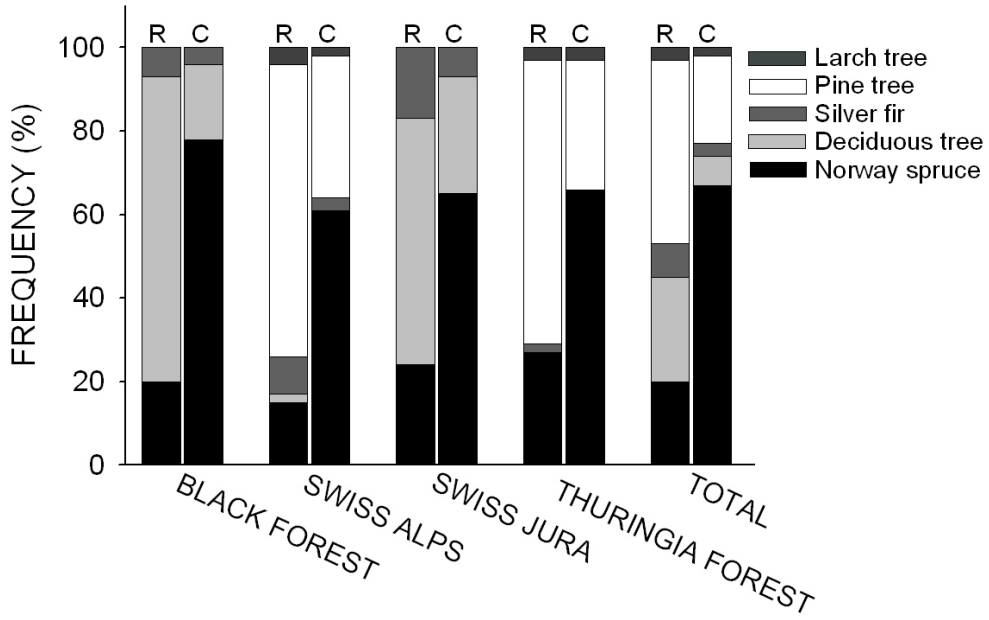
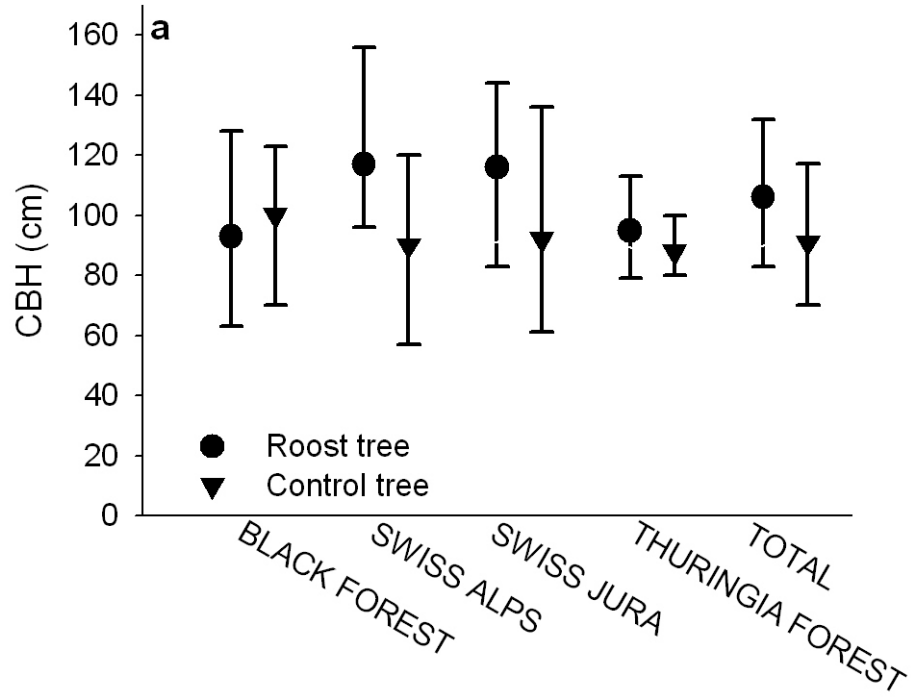


Figure 2. *Percentages of tree species of the 508 roost and matched control trees in the four study sites. The percentages sum up to 100% separately for roost (R) and control (C) trees.*



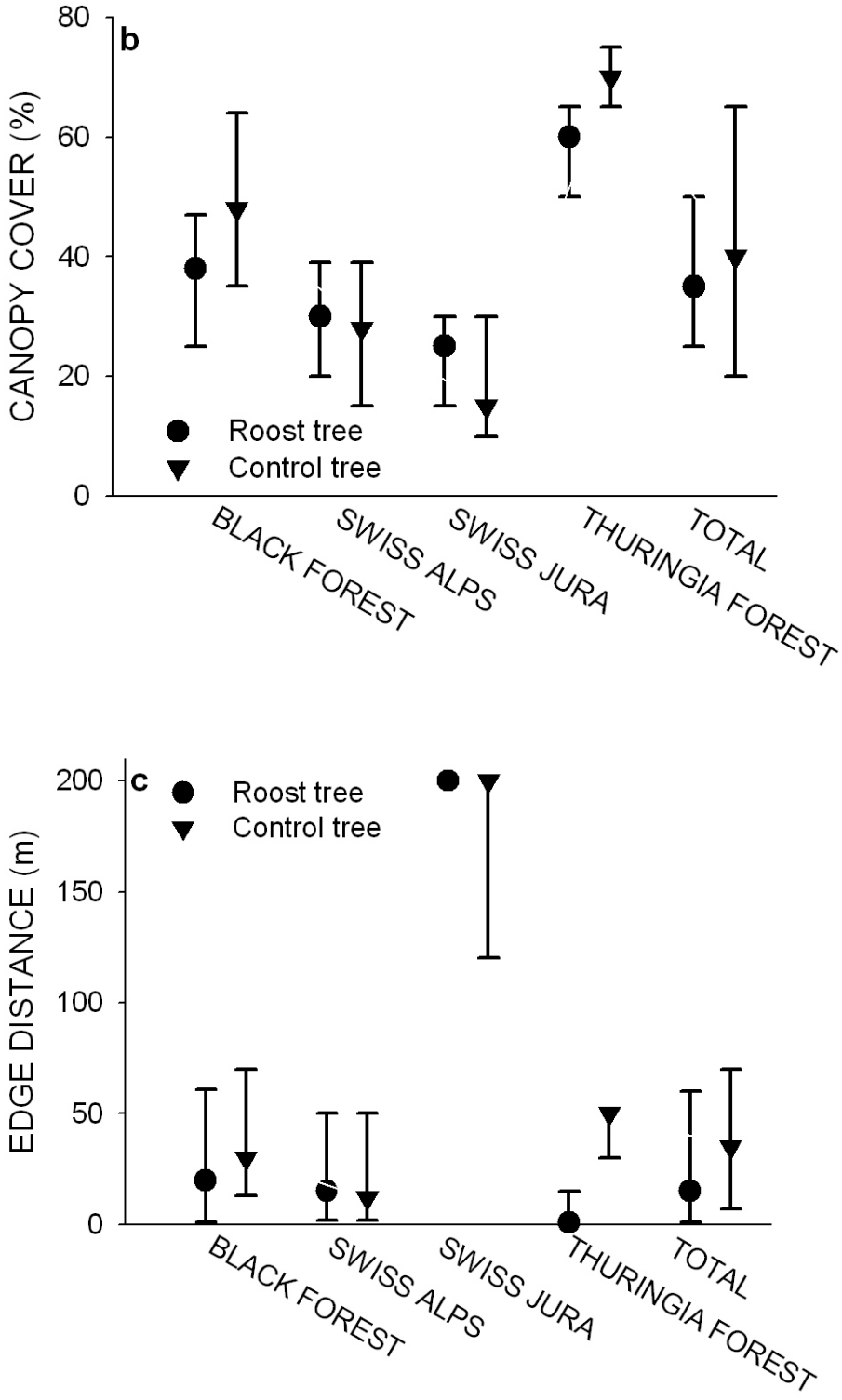


Figure 3. *(a) Circumference at breast-height CBH (in cm) of the 508 roost and matched control trees, (b) canopy cover (%), and (c) edge distance (m) in the surroundings of the 508 roost and matched control trees in the four study sites. The median, 25th and 75th percentiles are shown.*

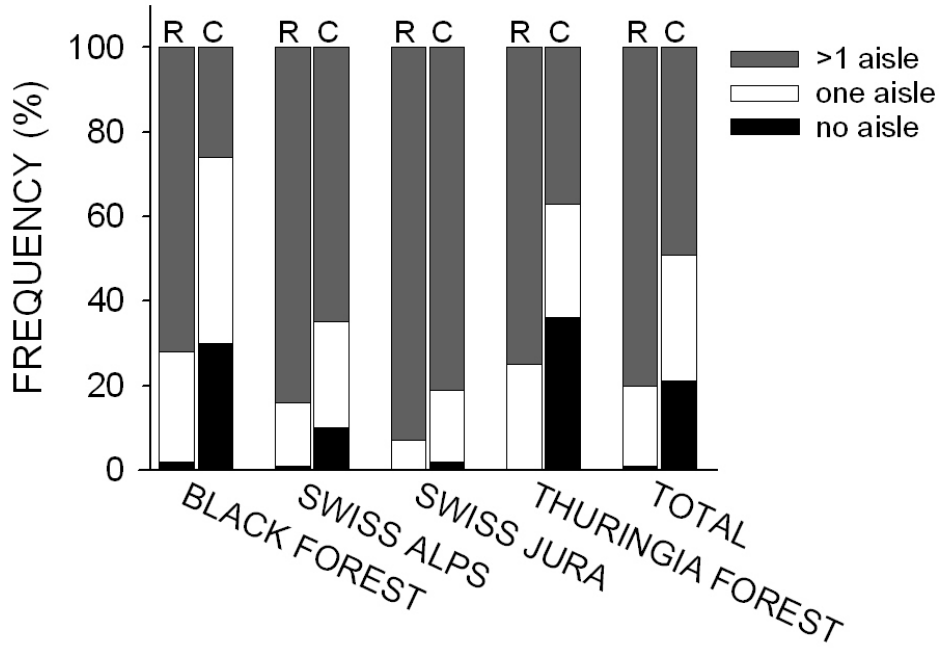
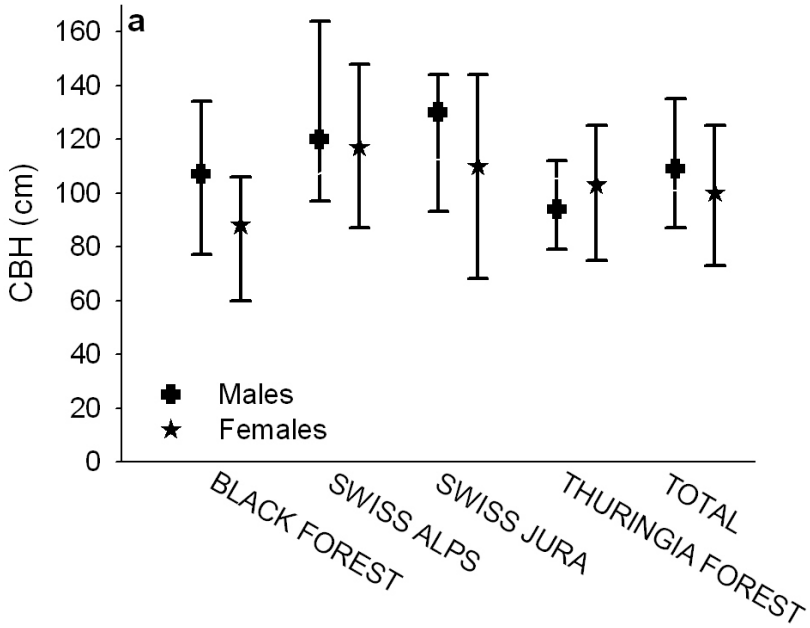


Figure 4. *Occurrence of forest aisles (none, one, >1) in the surroundings of the 508 roost and matched control trees in the four study sites. The percentages sum up to 100% separately for roost (R) and control (C) trees.*



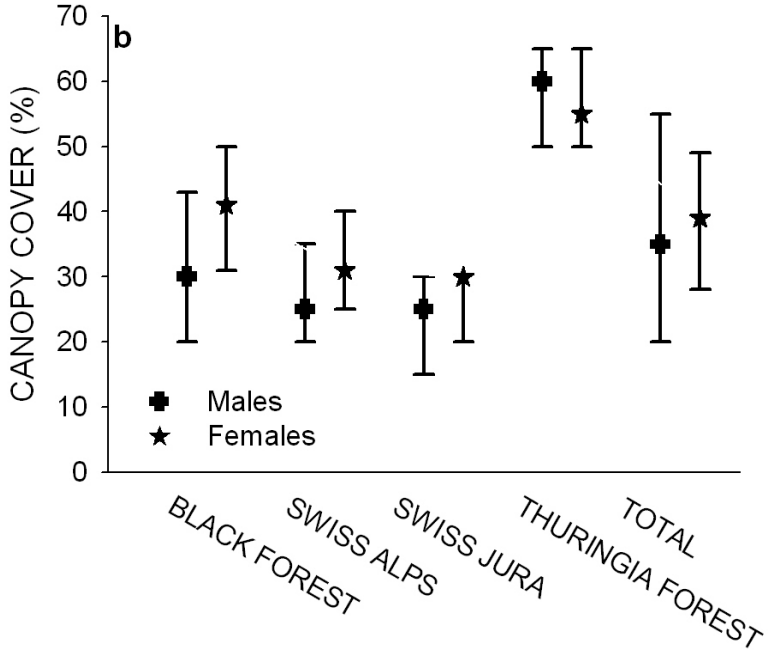


***Figure 5**. (a) Circumference at breast-height CBH (cm) of the 508 trees used by males and females, and (b) canopy cover (%) in the surroundings of the 508 trees used by males and females in the four study sites. The median, 25th and 75th percentiles are shown.*

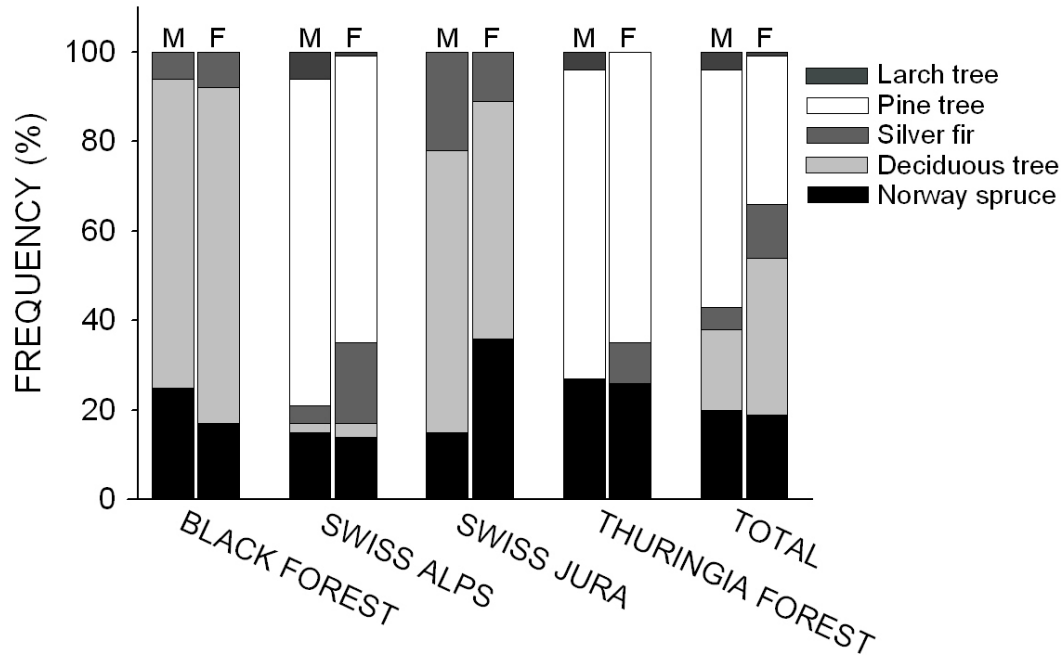


***Figure 6.** Percentages of tree species of the 508 trees used by males and females in the four study sites. The percentages sum up to 100% separately for trees used by males (M) and females (F).*

Paper III

Effects of recreation and hunting on flushing distance of capercaillie

In press as:

Dominik Thiel[1, 2], Emmanuel Ménoni[3], Jean-Francois Brenot[3], and Lukas Jenni[1]. Effects of recreation and hunting on flushing distance of capercaillie. Journal of Wildlife Management, in press.

[1]Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

[2]Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

[3]Office National de la Chasse et de la Faune Sauvage, Station des Pyrénées, Route Nationale 117, F-31800 Villeneuve de Rivière, France

Abstract

The capercaillie (Tetrao urogallus) in Central Europe is an endangered species of grouse that is thought to be highly susceptible to human disturbance, and this may have caused local populations to decline. We investigated the behavioural response of capercaillie in the Black Forest/Germany and in the French Pyrenees to an off-trail hiker by measuring flushing distances. Flushing distance varied with capercaillie sex, visibility of the hiker, intensity of winter tourism and hunting pressure. Independent of the study area, males flushed at consistently longer distances than females, and lower visual blocking between bird and hiker resulted in longer flushing distances. Capercaillie flew at longer distances from an approaching hiker in areas with high intensity of winter tourism or hunting pressure, than in undisturbed areas. We recommend to establish regulations requiring hikers to stay on trails and to close trails where inter-trail-distances fall below 100 m (90% of all flushing events appeared within 50 m). Furthermore, by the planting or preservation of evergreen conifer trees in dense rows along critical parts of disturbance sources, the degree of visibility between capercaillie and hiker can

be reduced, which would increase habitat for capercaillie in forests with predictable recreation activities.

Introduction

Outdoor recreation is a significant conservation problem for many wildlife species (Czech 2000), and a documented cause of population declines in endangered species (Venizelos 1991). To foster coexistence of humans and wildlife, species-specific knowledge about the susceptibility of wildlife to recreation is required (Taylor and Knight 2003, Blumstein et al. 2005). In general, humans as hikers in wildlife habitats are recognized as potential predators (Beale and Monaghan 2004). Once confronted with a predator, animals have the choice to flee, fight or hide, involving the animal in a trade-off between minimizing the costs of fleeing while maximizing its chances of survival. Flushing as a local-scale and immediate behavioural response is an outcome of this trade-off. Flushing distances have been used as an important measure to define and justify buffer zones to disturbance-free areas for wildlife species, where measurements of alert distances or other behavioural responses are impossible (Blumstein et al. 2003).

The capercaillie (*Tetrao urogallus*) is considered to be highly susceptible to human recreation activities. It is the world's largest grouse inhabiting boreal and mountainous coniferous forests in the Palaearctic and has been experiencing significant population declines over much of its European range for decades (Storch 2000). Large-scale habitat fragmentation and degradation are the main causes for this population decline, which has led to this species being listed in national red data books of western, central and south-eastern European countries (Storch 2000). Recreation such as winter tourism is viewed as an additional serious threat to local capercaillie populations. Unfortunately, only a few studies have investigated the responses of capercaillie to recreation. These studies documented a local decline in capercaillie numbers (Brenot et al. 1996) or the abandonment of lek sites (Labigand and Munier 1989, following an increase of winter tourism intensity. Studies investigating the direct behavioural responses of capercaillie to recreation are still lacking, although such studies are urgently needed for management plans aiming to stop population declines.

The capercaillie is likely to be sensitive to human disturbance for several reasons. (1) Capercaillie are large birds, and several studies have confirmed that alert- and flushing distances increase with body size (Fernandez-Juricic et al. 2001, Fernandez-Juricic et al. 2004, Blumstein et al. 2005). (2) The capercaillie is a prey species of several large aerial and terrestrial predators (Gjerde and Wegge 1989, Kurki et al. 1997), and is still a game species in some countries (Austria, France). (3) Habitat of capercaillie often overlaps with skiing areas (snow-rich mountain ridges, open forests, forest aisles). (4) Some outdoor recreational activities, such as back-country skiing and the increasingly popular snow-shoeing in, until now, relatively unexploited forests, are usually conducted off-trail. They are, therefore, an unpredictable disturbance source to which wildlife cannot readily become accustomed (Whittaker and Knight 1998, Miller et al. 2001).

Such recreation activities in winter are problematic, because winter is the most critical time of the year with high energy demands for many wildlife species. The energy intake of capercaillie in winter is limited due to the low energy content of conifer needles, the only winter food for capercaillie

(Lindén 1984). Therefore, capercaillie tend to minimize energy expenditure in winter by reducing their spatial and temporal activity (Gjerde and Wegge 1987, Storch 1995). Recreation activities resulting in increased flight activity are therefore a critical additional energy-robbing factor to which capercaillie are not adapted.

To better understand the susceptibility of the capercaillie to recreation in winter, we (1) investigated the critical distance at which capercaillie flush from hikers, (2) identified factors influencing flushing distances, and (3), in particular, assessed the impact of winter tourism and hunting pressure on flushing distance.

Study areas

The study was conducted in 3 different capercaillie populations in Western Europe: in the Black Forest, Germany (47^{O}51'N, 08 ^{O}00'E), and in 2 study areas in the French Pyrenees (42^{O}43'N, 01 ^{O}00'E; Fig. 1). These populations inhabit coniferous forests on mountain ranges.

In the Black Forest study area (11 km^2) the investigated forests range between an elevation of 1,000–1,400 m, and are dominated by dense forest stands of Norway spruce (*Picea abies;* 49%), European silver fir (*Abies alba*; 19%), and common beech (*Fagus sylvatica*; 22%; Suchant et al. 2003). Although forests are used for forestry extensively with mainly selective tree cutting and small-scale clear-cuts, forests are multi-layered and highly structured. Some large forest openings (>1 ha) have been caused by recent storms. Recreation in late autumn and winter was mostly restricted to winter tourism, and varied from intensively used hiking trails and skiing resorts with cross-country trails and downhill ski-runs, to predominantly recreation-free forests. Most winter tourism activities were on-trail. Off-trail activities (e.g. snow-shoeing, back-country skiing) in general are becoming more popular and frequent in the Black Forest, but were still relatively rare at the time of this study. Population size of capercaillie in the Black Forest is estimated to be 500–600 individuals (Braunisch and Suchant 2006), and belongs to the subspecies *T. urogallus major* (mean body weight of males 4 kg, of females 2 kg; Glutz von Blotzheim et al. 1973). Hunting of capercaillie in Germany has been prohibited since 1964.

In the French Pyrenees, we investigated 2 independent study areas, Beille and Esbas, with no short-term exchange of capercaillie between them (E. Ménoni, unpublished data). Within the study area Beille (39 km^2), data were collected in 5 study plots: Beille-Nord, Beille-Sud, Bourbourou, Campalou and Génibres. In the study area Esbas (29 km^2) we used 3 study plots (Esbas, Luchon, Sajust). Distances between the study plots ranged from 2–15 kilometers in both Pyrenean study areas. Due to the limited spacing behaviour of capercaillie in winter (Gjerde and Wegge 1987, Storch 1995), movements of >2 km are uncommon, thus reducing the probability of observing the same bird in different study plots.

Vegetation and topography of the Beille study plots on a plateau at elevations between 1,700–2,000 m were very similar to each other. They mostly consisted of young pine forest patches of 1–100 ha (<90 years, Mountain pine *Pinus uncinata*) up to the tree line with a small proportion of old trees (>200 years). Forests were well structured and interspersed with grazed meadows and small bogs, but without forestry activity. Although hunting was allowed in all 5 study plots, winter tourism was the predominant recreation activity in late autumn and winter and varied considerably between the study

plots. This pattern is due to the presence or absence of cross-country skiing tourism facilitated by large parking areas and other winter tourism facilities.

The study area Esbas ranged between an elevation of 1,300–2,000 m and differed from Beille both in tree species composition and slope: European silver fir and common beech were the most common tree species in similar proportions, with some European mountain ash (*Sorbus aucuparia)* and birches (*Betula pendula, Betula pubescens)*. Forested slopes were steep, up to 50°. The dominantly old growth forests were multi-structured with many natural treeless avalanche aisles, and some forestry activity by selective tree cutting of mature trees in 1986–1995. Winter tourism was almost non-existent, but hunting pressure on capercaillie varied among the study plots. Hunting is only allowed for capercaillie males from mid-September until late October and is usually conducted with the aid of pointing dogs. Hunting pressure depends on hunting law and access roads. Hunting activity for other game species continues until early winter, usually ending with the first heavy snow falls in December.

The population size of capercaillie *T. urogallus aquitanicus* in the entire range of the Pyrenees is approximately 3,500 birds. Body size of the Pyrenean subspecies (males 3.3 kg, females 1.6 kg; Ménoni 1991) is smaller than that of *T. urogallus major* in the Black Forest. All the given numbers probably underestimate the number of birds observed, because we collected data over several winters, including some years with high reproductive success.

Methods

Data collection

For several reasons (nature conservation aspects, reduced visibility in forests, cryptic plumage and shy behaviour of capercaillie), we could not conduct standardized flushing experiments. Furthermore, the use of GPS or similar technology for accurate and frequent monitoring of wildlife responses to human activity such as used in elk (*Cervus elaphus,* Preisler et al. 2006) was impossible, because the bearing quality of GPS/Satellite technology in capercaillie forests is too low (D. Thiel, unpublished data). Therefore, we were not able to determine alert distances or distances moved after being flushed.

In the Black Forest, we collected data of capercaillie flushed incidentally during (a) a feces-sampling study and (b) a radio-tracking study in the years 2003–2005. During the feces-sampling study, we walked off-trail along contour lines through forests within known capercaillie distribution areas. We reduced the probability of re-sampling the same individuals by visiting each site only once in early winter (November–December) and once in late winter (February–March). During the radio-tracking study, we visited 14 radio-equipped capercaillie every 3–5 weeks during autumn and winter to sample their fresh feces for physiological measurements, thereby usually flushing the birds. In 58 cases, a person walked straight towards a radio-equipped bird with known position. We, therefore, could determine (a) whether these birds flushed without being detected and (b) whether the distribution of flushing distances differed from those accidentally flushed, which could be caused if the latter were the more sensible ones.

In the Pyrenees, we used observations over a time period of 13 years (1984–1996). A single observer walked off-trail 1–2 times/year along contour lines through forests in capercaillie core areas

(see methods in Brenot et al. 1996). This reduced the probability of re-sampling the same individual, even though certain individuals could have been observed multiple times over the years.

Because of our aim to investigate sensitivity of capercaillie to hikers during the period of hunting and winter tourism, we only considered the period between late autumn and late winter (October–March). This also ensured that climatic conditions and vegetation condition remained similar, with deciduous trees already without leaves or losing them. Snow covered all ground vegetation during the majority of the study period in all 3 study areas. The only hiding possibilities for capercaillie were conifer trees with dense branches down to the ground.

We measured the distance (m) between the hiker and the bird at its take-off position in all years with (1) a range finder (Nikon, Laser-400) in the Black Forest by Dominik Thiel and 3 trained field assistants, and (2) with foot steps in the Pyrenees by Jean-FranÇois Brenot (Beille) and Emmanuel Ménoni (Esbas). In the Black Forest, we also measured distances with a range finder in a few cases where birds were detected without flushing. In those cases, birds were not forced to flush and were not included in the analysis. Other cases, where capercaillie would escape by foot on the ground from a hiker instead of flying are very unlikely. This is first due to the fact that capercaillie during our study period could hardly hide on the ground, and secondly, capercaillie in winter (especially females) mostly avoid the ground (Klaus et al. 1989). In the Black Forest, we also measured flushing distances of capercaillie observed from a vehicle driving along forest roads while checking mist-nets for capercaillie for a radio-tracking study.

For each observation of a flushed bird, we recorded 6 predictor variables (Table 1). The sex of the capercaillie flushed was determined on the basis of body size and colour of plumage (small-sized cryptic-brownish females, large darkish-coloured males). Confusion of female capercaillie with other grouse species was not possible because capercaillie were the only grouse species in all study areas. We included a measure of vegetation density because vegetation blocks visual contact between a hiker and wildlife, and thus affects sensitivity to intrusion (de Boer et al. 2004). In the Black Forest, we established a categorical predictor variable VISIBILITY at the point the hiker located a flushed capercaillie, scoring the degree of visual contact between bird and hiker at 4 levels: (1) nothing blocking the view between bird and hiker, (2) bird hidden in trees but hiker exposed in the open, (3) bird and hiker partly hidden by trees, (4) bird exposed in the open and hiker sitting in a car. In the 2 Pyrenean study areas, we measured forest canopy cover CANOPY between hiker and flushed bird as a continuous predictor variable. Because most trees in the Pyrenean study area were evergreen conifer trees with branches almost down to the ground, canopy cover was a good measure of the visual contact between bird and hiker. For each bird we recorded whether it was on the ground or perched on a tree (PERCH LOCATION).

In the Black Forest, the variable RECREATION roughly scored the quantity and frequency of winter tourism intensity based on our almost daily field observations during the radio-tracking study (Table 1). The level “high” was assigned for daily tourism activity with high intensity of a large number of people, facilitated by easy access by roads, extensive parking areas and a dense network of hiking trails, cross-country tracks, or ski-runs. The level “moderate” represented irregular tourism activity with fewer visitors and “low” stands for only rare or no visitation by people. The levels of RECREATION in the Black Forest were assigned at the scale of forest stands (about 2 to several 1,000 ha, usually

surrounded by treeless pastures) because tourism intensity varied greatly at a small scale due to the heterogeneous topography. In the Pyrenean study area Beille, where only winter tourism varied among study plots, the corresponding variable RECREATION had the same 3 levels based on our observations during the field work (Brenot et al. 1996) but they were assigned at the level of study plots due to the relatively homogenous topography (Table 1). In the Pyrenean study area Esbas, hunting pressure varied greatly between study plots, but winter tourism was almost non-existent. We therefore introduced the variable HUNTING with the level "high" for 2 study plots with high hunting pressure, and the level "no" for 1 study plot without hunting activity. The continuous variable DATE was computed as a transformed Julian date by numbering each day from 1 October (day 1) to 31 March (day 182) independent of the year.

Statistical analysis

We used General Linear Model GLM (Type I) to identify factors affecting flushing distances. Because predictor variables (recreation vs. hunting pressure) and the method of measuring flushing distances were not identical in the 3 study areas, we analyzed the 3 data sets separately.

In all 3 analyses, the order of the predictor variables (Table 1) and their 2-way interaction terms were identical. In a first step, we included all 6 predictor variables and all 15 possible interaction terms, except for the interaction SEX×PERCH LOCATION in the study area Beille with sample sizes per level <5. After backward elimination of non-significant interaction terms, the final model included all main effects, and all interaction terms with $P \leq 0.05$.

We tested whether flushing distance differed among individuals by analyzing flushing distances from 14 radio-tracked capercaillie from the Black Forest (7 males, 7 females, mean number of flushing events per bird = 5.7, ranging between 1–11). We established a linear mixed model with the 2 most important predictor variables from the Black Forest (SEX and VISIBILITY) and its interaction term as fixed factors and with the individual bird INDIV as random factor. Due to the low sample size of flushing distance of radio-tracked birds, we could not add more predictor variables without strongly reducing statistical power. A linear model was built with the same fixed factors but without the random factor INDIV. We compared the 2 models using a likelihood ratio test to assess whether there was significant variation among the individuals.

In all analyses, the residuals of the response variable flushing distance were normally distributed; thus, no transformation was necessary. We used GenStat for Windows version 7.3 (Payne 2003) for all analyses.

Results

For all study areas combined, observed capercaillie flew at a mean distance of 27 ± 0.6 m (SE; n = 752) with a range of 1–104 m, and 90% of all flushing events happened at a distance < 50m. In the Black Forest, mean flushing distance of capercaillie was 30 ± 1.2 m, in Beille 24 ± 0.6 m, and in Esbas 27 ± 1.4 m. Flushing distance of males (31 ± 0.9 m) was longer than for females (22 ± 0.6 m; Fig. 2a, Tables 2–4). Flushing distances of the 14 radio-tracked birds in the Black Forest with known positions (males: 38 ± 4.0 m, females: 23 ± 2.5 m; Fig. 2b) were similar to those with birds flushed incidentally in this study area (males: 35 ± 1.8 m, females: 25 ± 1.3 m).

In the Black Forest, we observed 68 birds out of 331 (21%) that did not flush upon detection. The mean distance between the hiker and those males that did not flush (35 out of 164) was longer (65 ± 9.6 m) than the corresponding value for females (33 out of 167; 30 ± 6.6 m; $F_{1,66}$ = 8.65, P = 0.004).

Visibility between bird and hiker influenced flushing distance in all study areas (Tables 2–4; visibility score for the Black Forest; canopy cover as a surrogate in the Pyrenees). Flushing distance increased with decreasing visibility between bird and hiker for males and females in the Black Forest and in Beille (Fig. 3–4). In Esbas, flushing distance differed slightly with canopy cover depending on group size (Table 4). Flushing distance decreased with increasing canopy cover for single capercaillie, whereas flushing distances for capercaillie in groups did not change with canopy, except in very dense forests, where flushing distance was shorter.

Winter recreation intensity (Black Forest and Beille) and hunting pressure (Esbas) influenced flushing distance. In the Black Forest, the effect of recreation varied with sex and group size (Table 2). The mean flushing distance of males increased with increasing recreation intensity, whereas the corresponding value for females increased only slightly from low to moderate recreation intensity (Fig. 5a). For single capercaillie, flushing distance was similar for all recreation intensities (Fig. 5b), but for groups of 2 or more birds (range = 2–7), flushing distance increased with increasing recreation intensity (Fig. 5b). In Beille, the effect of recreation on flushing distance differed with date from December to March (Table 3), and showed an irregular pattern. The mean flushing distances in study plots with low recreation intensity increased from early winter (18 ± 1.7 m in December/January) to late winter (February/March, 24 ± 1.0 m). The corresponding values in study plots with moderate recreation intensity decreased from 26 ± 1.2 m in February to 13 ± 1.1 m in March, whereas mean flushing distances in study plots with high recreation intensity remained at a high level throughout the winter (25 ± 1.8 m in December/January, and 26 ± 1.9 m in February/March). Capercaillie in Esbas study plots with no hunting flushed at shorter distances than those in the study plot with high hunting pressure, but this hunting effect was sex-dependent. For females, mean flushing distances were similar in study plots without and with high hunting pressure (22 ± 1.6 m and 18 ± 3.3 m, respectively). Capercaillie males flushed at much longer distances in the study plot with high hunting pressure (48 ± 4.3 m) than in plots without hunting (29 ± 2.3 m; Table 4). The effect of date in Esbas was strongly influenced by hunting (Table 4). Flushing distances of capercaillie in plots with high hunting pressure were highest in late autumn when hunting was in progress, and continuously decreased over time after hunting was closed (Fig. 6). The corresponding values for capercaillie in plots without hunting pressure remained at a low level from October to March (Fig. 6). The effect of hunting on flushing distance varied further with perch location (Table 4). Flushing distance of capercaillie perching in trees did not differ with hunting pressure (28 ± 1.8 m without hunting and 26 ± 4.8 m with high hunting pressure). The corresponding values for birds on the ground increased from no hunting (21 ± 1.9 m) to high hunting pressure (36 ± 5.2 m).

Flushing distance was further influenced by group size, but the effect showed an irregular pattern (Table 3–4). In Beille, flushing distance was slightly shorter for capercaillie in groups, than for single capercaillie, but this pattern was sex-dependent. In capercaillie males, mean flushing distance was longer for single males (28 ± 1.2 m) than for males in a group (23 ± 1.4 m). For females, these

values did not vary with group size (21 ± 0.9 m and 22 ± 1.1 m, respectively). In Esbas, the effect of group size on flushing distance was sex-dependent (Table 4). Single males flushed at shorter distances than males in a group (28 ± 3 m, and 39 ± 3.1 m), whereas the corresponding values for single females and females in a group did not differ (22 ± 3.2 m, 21 ± 1.6 m). Single capercaillie on the ground flushed at longer distances than those perched in trees (29 ± 3.4 m and 24 ± 2.9 m). For capercaillie in groups, this relationship was reversed (20 ± 2.0 m for birds on the ground, and 29 ± 2.1 m for birds in trees).

Differences between individuals

There was no variation in flushing distance among the 14 radio-tracked individuals (likelihood ratio test: χ^2_4 = 0.11, P = 0.74). Males (n = 34; 37 ± 3.3 m) flushed at much longer distances than females (n = 46; 25 ± 2 m; Wald χ^2_1 = 8.91–11.68, P < 0.01).

Discussion

The distance at which capercaillie flushed from an off-trail hiker in late autumn and winter varied mainly with sex, degree of visual blocking between bird and hiker and degree of human outdoor activity (recreation and hunting pressure), while the effect of date, group size and the position of the bird was modifying. Patterns were similar in all 3 or at least 2 study areas. Generally, flushing distance was longer for capercaillie males in hunting areas (Esbas), in areas with high recreation intensity (Black Forest) and in open forests (Black Forest, Beille), than for females under the same conditions. Independent of sex, flushing distance was longer in areas with high human intensity and where birds were not hidden by trees.

The comparison of flushing distance of accidentally flushed birds with radio-equipped birds demonstrates that the sample of flushed birds was not biased in favour of particularly sensible birds (i.e. towards longer distances) or that birds flushing at longer distances have been missed (i.e. towards shorter distances).

Sex-specific flushing distances

In all 3 populations and independent whether the birds were radio-equipped or not, males flushed at longer distances from a single hiker than females, as already described by Catt et al. (1998) in Scottish capercaillie. Several studies have found a positive relationship between body mass and alert- or escape distances in different bird species (Blumstein et al. 2005, Laursen et al. 2005). This pattern was explained by a greater visual acuity of larger species (Kiltie 2000), resulting in a longer detection distance (Fernandez-Juricic et al. 2001). In this study we found a similar pattern at the intra-specific level between sexes and subspecies. Males are twice the size of females, and flushing distances of females in all study areas were 22–36% shorter than those of males. Flushing distances of the larger and heavier subspecies *T. urogallus major* of both sexes exceeded those of the smaller subspecies *T. urogallus aquitanicus*. In bird species with a smaller sex-dimorphism than in capercaillie, no difference in flushing distance between sexes was found (Mexican spotted owls *Strix occidentalis lucida*, Swarthout and Steidl 2001; small raptors, Holmes et al. 1993).

Intra-specific differences in sensitivity to hikers can also be caused by temporally varying starvation risk and energetic demands. In oystercatchers (*Haematopus ostralegus*), hiker tolerance and the negative effect of flushing on body condition are larger in late winter (Stillmann and Goss-Custard 2002) and under poor feeding conditions (Goss-Custard et al. 2006). In contrast to oystercatchers, capercaillie do not experience difficulty in finding enough food since conifer needles are their only, but superabundant, food source in winter. However, the energy intake of capercaillie in winter is severely restricted due to the low quality of conifer needles and difficulty in digesting them (Andreev and Lindén 1994). The constraints to meet energy demands are more severe for capercaillie hens than for males, because females have a higher 'lower critical temperature' (Rintamäki et al. 1984), a higher heat loss in relation to body size according to Rubner's surface rule, and a higher standard metabolic rate / kg body weight (Rintamäki et al. 1984) than males. Therefore, hens may try to avoid energy-expensive flights to a greater extent than males, and are less sensitive to human activity in order to minimize energy expenditure.

Habituation of females (but not of males) to humans could be another possible reason for their lower sensitivity to hikers. However, if this was the case, we would not expect visibility between hiker and bird to have the same effect on the sensitivity to hikers in both males and females.

One could argue that the larger males have longer flushing distances because flushing males produce more noise while flushing compared to smaller and quieter females with shorter flushing distances, and are therefore more likely to detect. Our findings and experiences contradict this idea: (1) we observed not only males but also females at relatively long distances of > 40 m (Fig. 2a). (2) The flushing distances of the radio-tracked individuals showed the same sex-specific pattern of flushing distance (Fig. 2b). (3) The mean distance between the hiker and those males in the Black Forest that did not flush on detection was 35m longer than the corresponding value for females, confirming that at certain distances females do not flush, when males do.

Effects of visibility between bird and hiker on flushing distances

In all study areas, visibility influenced flushing distance. The shortest flushing distance of capercaillie was observed in dense forests in Beille or in the Black Forest when the hiker was hidden in a car. This was confirmed by other studies showing that flushing distances of birds and mammals were much shorter when vehicles rather than hikers were involved (Taylor and Knight 2003, Rees et al. 2005). The longest flushing distances occurred in open forests with few trees interrupting the view between bird and hiker. This is in agreement with other studies showing that the physical structure of vegetation and vegetation density affected hiker tolerance of several bird and mammal species (Fernandez-Juricic et al. 2004). All these findings confirm that the visibility of a hiker is an important factor determining sensitivity to recreation in wildlife.

Consequences of recreation and hunting pressure on flushing distances

In forests with recreation and hunting pressure, flushing distances were longer than in undisturbed forests. In the Black Forest, mainly males and capercaillie in groups flushed at longer distances in forests with intensive recreation than in undisturbed forests. Females seemed to be less sensitive to hikers than males, which again can be attributed to the pronounced sex-dimorphism. However, the

longer flushing distances between capercaillie and hikers in highly disturbed forests indicate that capercaillie do not become accustomed to recreation. These results are probably caused by the unpredictability of off-trail hikers, where habituation for wildlife is not possible (Whittaker and Knight 1998, Miller et al. 2001).

Many other studies on wildlife have shown that flushing distance increased with hunting pressure (Madsen and Fox 1995, de Boer et al. 2004, Laursen et al. 2005). Interestingly, in our study in Esbas, hunting pressure increased flushing distance only in males, only during the hunting season in late autumn, and only in birds on the ground. Capercaillie males almost doubled their flushing distance during the hunting season, which is similar to the results found in geese (Madsen and Fox 1995). The fact that only males reacted with longer flushing distances to hunting pressure could be due to the fact that only males are hunted, or due to the sex-dimorphism, where females rely on camouflage and aim to avoid energy-costing flights.

Management implications

Based on our results, we recommend the following 3 habitat management strategies to reduce the negative effects of recreation on capercaillie in winter. (1) To avoid potential disturbances from unpredictable off-trail activities in capercaillie core areas, regulations requiring recreationists to stay on trails and other tourist facilities are implemented and kept under surveillance. (2) To reduce the degree of visibility between capercaillie and recreationists, evergreen conifer trees may be planted or preserved in a dense row along critical parts of potential disturbance sources. Such critical parts include for example forest stands with ideal foraging or roosting trees (pine trees, *Pinus spp.*; or European silver fir) adjacent to trails crossing ideal open capercaillie habitat without visual blocking structures. (3) To assure a sufficient area of undisturbed habitat, an increase in number of trails is to be avoided and trails may even be closed. This may be particularly appropriate where capercaillie winter core areas are strongly reduced by dissecting trails or where inter-trail distances are below 100m (90% of all flushing distances < 50m). A disturbed area of 50 m along cross-country tracks in one part of our study area in the Black Forest would cover 16% of 821 ha or 29% with a disturbed area of 104 m (maximum flushing distance, n = 752). This indicates that recreation can lead to a marked reduction in the availability of undisturbed habitat, even if these values are computed from capercaillie flushing from an off-trail hiker, which probably results in longer flushing distances than those resulting from a predictable disturbance source. Because alert distances are longer than flushing distances (Fernandez-Juricic et al. 2001), we therefore consider our recommendation based on flushing distances as a minimum for dense forests which should be doubled (100m each side; 100% of all flushing distances) in more open forests. Other wildlife species would probably also benefit from these capercaillie-based management implications, because capercaillie is an umbrella species with habitat requirements of several red-listed mountain bird species, such as hazel grouse (*Bonasa bonasia)* and woodcock (*Scolopax rusticola*; Suter et al. 2002).

Acknowledgments

DT thanks Samuel Ehrenbold, Ruedi Meier, Peter Nyffeler, Tobias Roth, Thomas Sattler and Thomas Wicki for their support in the field. We also thank Michael Schaub for assistance in data analysis. For

their helpful comments to this manuscript, we thank Penelope Barnett, Pierre Defos du Rau, Christian Marti, Christine B. Müller, Ilse Storch, Philip Tipping and Niklaus Zbinden. DT is especially grateful to the foresters Wolfgang Ebser and Claudio Röhmer-Litzmann who supported this study in the Black Forest. The International Council for Game and Wildlife Conservation CIC and the Janggen-Pöhn-Foundation, Switzerland, financially supported DT. The Office National de la Chasse et de la Faune Sauvage ONCF financially supported JFB and EM.

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Table 1. *Predictor variables used to characterize flushing distance of capercaillie in the study area Black Forest/Germany (2003–2005) and in the 2 study areas Beille and Esbas in the French Pyrenees (1984–1996).*

Variable name	Definition	Study area
SEX	2 levels	Black Forest, Beille, Esbas
VISIBILITY	4 levels: see methods	Black Forest
CANOPY (in %)	Percentages of forest floor covered by trees	Beille, Esbas
PERCH LOCATION	2 levels: ground, on tree	Black Forest, Beille, Esbas
GROUP	2 levels: 1, >1	Black Forest, Beille, Esbas
RECREATION	3 levels: low, moderate, high	Black Forest, Beille
HUNTING	2 levels: no, high	Esbas
DATE	transformed Julian date, see methods	Black Forest, Beille, Esbas

Table 2. *Effect of the predictor variables and their 2-way-interactions on flushing distance (m) of capercaillie in the Black Forest/Germany (n = 263) in 2003–2005. Estimates were calculated considering a reference value of zero for SEX(male), VISIBILITY (b & h exposed), PERCH LOCATION(ground), GROUP(1), and RECREATION(low). Abbreviations used in visibility levels are: b = bird, h = hiker.*

Variable	Estimate	SE	df	MS	F	P
Main effects						
SEX(female)	-6.70	3.93	1	7115	25.70	<0.01
VISIBILITY			3	2815	10.20	<0.01
b hidden, h exposed	-9.51	2.74				
b & h partly hidden	-7.60	3.17				
b exposed, h hidden in car	-23.61	4.56				
PERCH LOCATION(on tree)	-1.17	2.63	1	338	1.20	0.27
GROUP(>1)	-5.31	3.88	1	538	1.90	0.17
RECREATION			2	1128	4.10	0.02
moderate	0.11	3.79				
high	6.59	4.61				
DATE	-0.01	0.03	1	2	0.00	0.94
Interaction terms						
RECREATION × SEX			2	827	3.00	0.05
RECREATION(moderate) × SEX(female)	0.84	5.20				
RECREATION(high) × SEX(female)	-11.00	5.66				
RECREATION × GROUP			2	1818	6.60	0.00
RECREATION(moderate) × group	7.99	5.63				
RECREATION(high) × group	20.59	5.66				

Table 3. *Effect of the predictor variables and their 2-way-interactions on flushing distance (m) of capercaillie in Beille in the French Pyrenees (n = 335) in 1984–1996. Estimates were calculated considering a reference value of zero for SEX(male), PERCH LOCATION(ground), GROUP(1), and RECREATION(low).*

Variable	Estimate	SE	df	MS	F	P
Main effects						
SEX(female)	-7.06	1.31	1	2612	27.30	<0.01
CANOPY	-0.32	0.05	1	5882	61.50	<0.01
PERCH LOCATION(on tree)	5.16	4.99	1	130	1.40	0.25
GROUP(>1)	-5.32	1.80	1	555	5.80	0.02
RECREATION			2	244	2.60	0.08
moderate	48.30	16.20				
high	16.40	15.30				
DATE	-0.01	0.05	1	305	3.20	0.08
Interaction terms						
SEX(female) × GROUP(>1)	6.20	2.37	1	541	5.70	0.02
RECREATION × DATE			2	452	4.70	0.01
RECREATION(moderate) × date	-0.34	0.11				
RECREATION(high) × date	-0.12	0.12				

Table 4. *Effect of the predictor variables and their 2-way-interactions on flushing distance (m) of capercaillie in Esbas in the French Pyrenees (n = 154) in 1984–1996. Estimates were calculated considering a reference value of zero for SEX(male), PERCH LOCATION(ground), GROUP(1), and HUNTING(no).*

Variable	Estimate	SE	df	MS	F	P
Main effects						
SEX(female)	-2.04	3.87	1	5400	30.00	<0.01
CANOPY	-0.23	0.11	1	328	1.80	0.18
PERCH LOCATION(on tree)	2.31	3.76	1	676	3.80	0.06
GROUP(>1)	-9.63	8.68	1	524	2.90	0.09
HUNTING(high)	36.08	6.52	1	938	5.20	0.02
DATE	-0.05	0.02	1	2328	12.90	<0.01
Interaction terms						
SEX(female) × GROUP(>1)	-11.79	4.85	1	987	5.50	0.02
SEX(female) × HUNTING(high)	-17.03	5.49	1	3679	20.40	<0.01
CANOPY × GROUP(>1)	0.18	0.15	1	789	4.40	0.04
PERCH LOCATION(on tree) × GROUP(>1)	14.59	4.97	1	1333	7.40	0.01
PERCH LOCATION(on tree) × HUNTING(high)	-6.93	6.27	1	1029	5.70	0.02
HUNTING(high) × DATE	-0.11	0.05	1	790	4.40	0.04

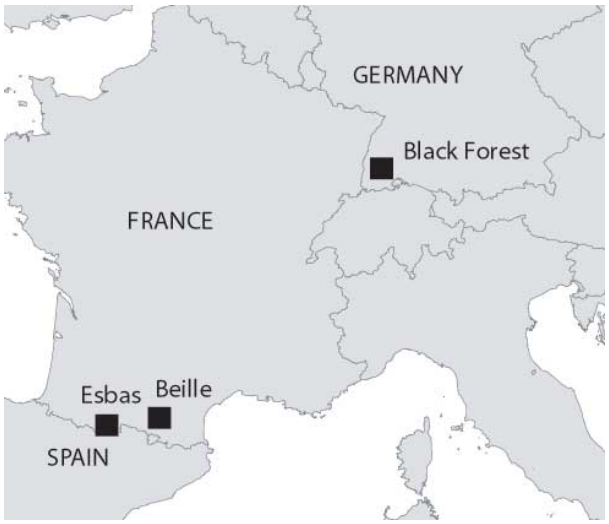

Figure 1. *Location of the 3 study areas Black Forest/Germany, and Beille and Esbas in the French Pyrenees in Western Europe, where data on flushed capercaillie were collected in late autumn and winter in the years 2003–2005 and 1984–1996 (© Institute of Cartography ETH Zürich).*

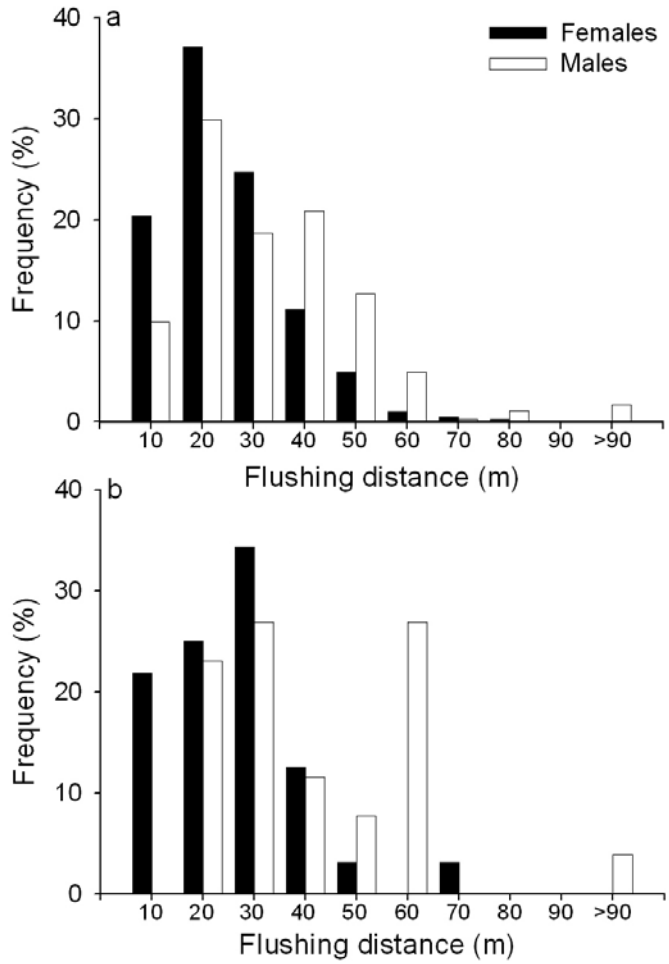

Figure 2. *Frequencies (%) of flushing distances grouped in categories of 10 m of females (black) and males (white) of (a) all 3 study areas combined (n = 752) in 1984–1996 and 2003–2005, and of (b) 14 radio-tracked capercaillie (n = 58) in the Black Forest/Germany in 2003–2005. Percentages per sex sum up to 100%.*

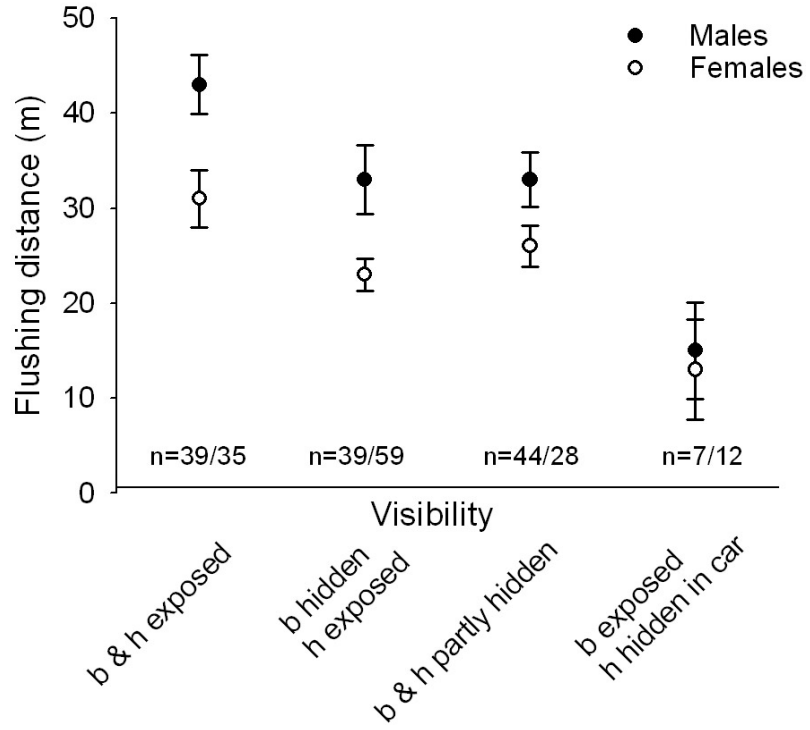

Figure 3. *Flushing distances (mean ± SE) of capercaillie males (filled circles) and females (open circles) in the Black Forest/Germany over 4 levels of visibility between bird (b) and hiker (h) in 2003–2005. Sample sizes are given for males/females.*

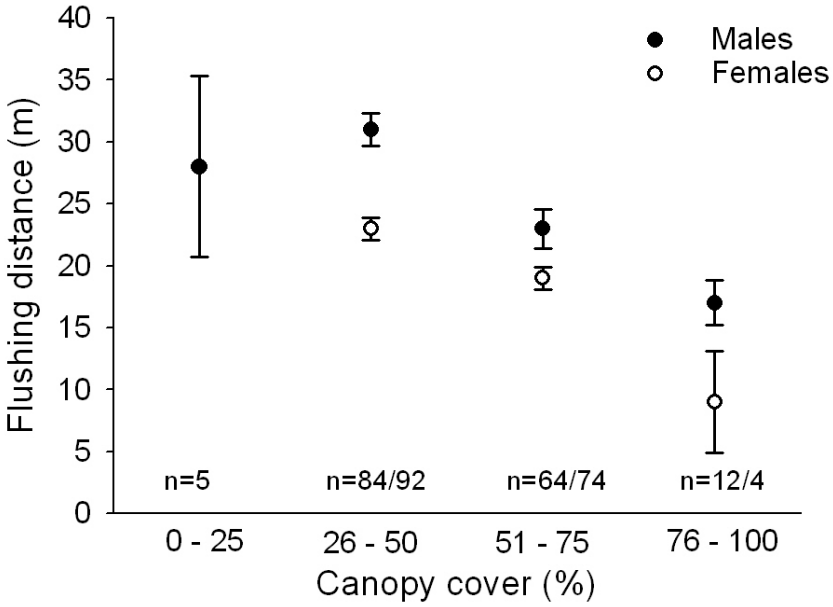

Figure 4. *Relationship between canopy cover and mean flushing distance (± SE) of capercaillie males (filled circles) and females (open circles) in the study area Beille/French Pyrenees in 1984–1996. Sample sizes are given for males/females.*

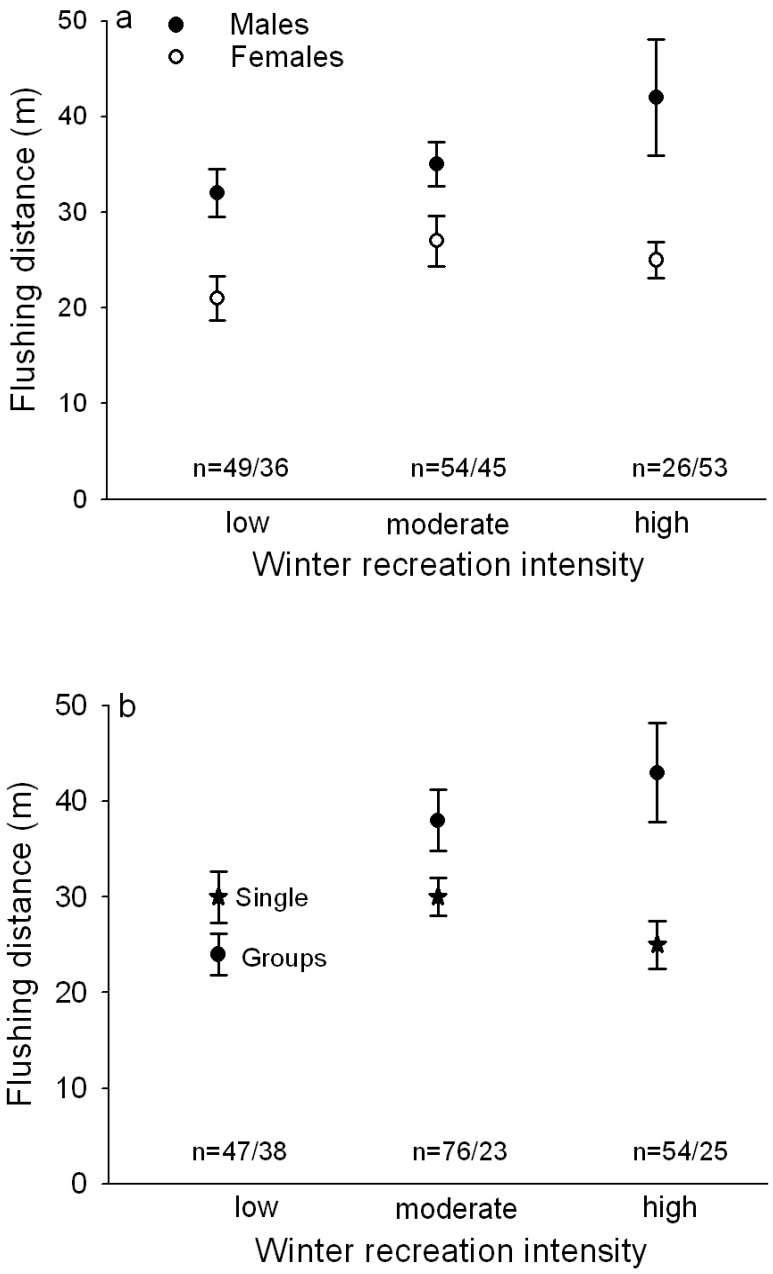

Figure 5. *Flushing distances (mean ± SE) of (a) capercaillie males (filled circles) and females (open circles), and of (b) single capercaillie (stars) and capercaillie in groups (filled circles) in the Black Forest/Germany in 2003–2005 among 3 winter recreation intensities. Sample sizes are given for (a) males/females and for (b) single capercaillie/capercaillie in groups.*

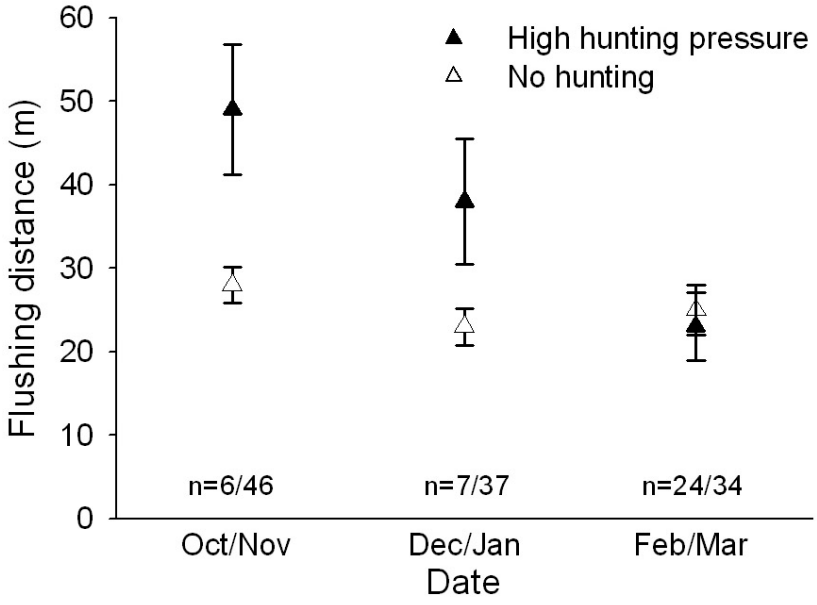

Figure 6. *Mean (± SE) flushing distances of capercaillie with high (filled triangles) and without (open triangles) hunting pressure for 3 time periods (late autumn, mid winter, late winter) in the study area Esbas/Pyrenees in 1984–1996. Sample sizes are given for capercaillie in areas with high/no hunting pressure.*

Paper IV

Ski tourism affects habitat use and evokes physiological stress in capercaillie *Tetrao urogallus*

To be submitted as:

Dominik Thiel[1,2] , Susanne Jenni-Eiermann[1], Veronika Braunisch[3], Rupert Palme[4] and Lukas Jenni[1]. Ski tourism affects habitat use and evokes physiological stress in capercaillie *Tetrao urogallus.*

[1]Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

[2]Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

[3]Forest Research Institute of Baden-Wuerttemberg FVA, Wonnhaldestr. 4, D-79100 Freiburg im Breisgau, Germany

[4]Institute of Biochemistry, Department of Natural Sciences, University of Veterinary Medicine, Veterinärplatz 1, A-1210 Vienna, Austria

Summary

1. Winter tourism in Central Europe is of great economical importance and of nature conservation concern. It affects areas with otherwise low human impact but with retreats for many species in an energetically demanding season of the year. Capercaillie are expected to be negatively affected by human recreation activities, which may have contributed to the population declines during the last decades.

2. We examined the effects of ski tourism on capercaillie habitat use and measured glucocorticoid levels as an indicator of stress in capercaillie droppings.

3. During three winters 2003–06, we radio-tracked 13 capercaillie. We sampled 396 droppings of them and additional individuals before and during the ski season in the Southern Black Forest/Germany. We used compositional analysis to test whether winter recreation intensity affected home range location and habitat use within home ranges, and applied a REML-analysis to identify factors influencing corticosterone metabolite concentration in droppings.

4. Capercaillie habitat use overlapped with skiing areas, but the latter did not affect home range location. However, within their home ranges, capercaillie preferred undisturbed forests and avoided areas with high recreation intensity during the ski season. Faecal glucocorticoid level of individuals in areas with no or low recreation intensity were significantly lower than those in areas with moderate or high recreation intensity during the entire period of the study period.

5. We conclude that ski tourism affects both habitat use and endocrine status in capercaillie including potential negative consequences on body condition and overall fitness. The reason that capercaillie use skiing areas despite the possible negative consequences is probably due to a lack of other high-quality but disturbance-free habitats.

6. *Synthesis and application.* This study demonstrates the value of using multiple methods applied on the same individuals to biomonitor impacts of human disturbance on free-ranging species. We recommend to keep forests inhabited by capercaillie free of tourism infrastructure, and to ensure undisturbed forest patches within skiing areas.

Introduction

Winter tourism takes place on large parts of snow-rich high-elevation areas. In Europe, ski tourism is one of the most important economic factors in alpine regions (Elsasser & Messerli 2001). Besides the infrastructures with buildings, car parks, hiking trails, ski-lifts, ski-runs and ski-tracks, off-trail activities such as paragliding and free-riding snow sports occur on an additional large area. Most winter tourism areas are located in rural landscapes with considerably lower recreation activity in summer. Such pristine areas often are essential habitats or retreats for rare or shy species, such as black grouse *Tetrao tetrix*, capercaillie *Tetrao urogallus*, red deer *Cervus elaphus* and chamois *Rupicapra rupicapra*. Winter tourism is of increasing conservation concern, because the quantity of winter sport activities and new outdoor sport types such as snow-shoeing vastly increased during the last decades. Outdoor recreation is a documented cause of population decline in endangered species (Venizelos 1991), and it is one of the main causes for the decline of federally threatened and endangered species in the United States (Czech 2000).

The response of free-ranging animals to human recreation activities has been extensively studied. They usually respond to the appearance of humans with an anti-predatory behaviour (Frid & Dill 2002; Beale & Monaghan 2004b). Human disturbance can cause animals to interrupt feeding behaviour, to flee (Thiel *et al.* 2007a), or abandon preferred habitats temporally or permanently (Skagen, Knight & Orians 1991; Fernandez-Juricic & Telleria 2000). Such direct behavioural responses can affect predation risk, energy intake and energy expenditure of the animal (Cassirer *et al.* 1992), and thus have direct fitness costs (Amo *et al.* 2006). As a physiological response to stressors, glucocorticoid hormones are secreted into the blood (corticosterone in birds; Sapolsky *et al.* 2000), a mechanism to adjust the behaviour and the physiology of the animal to prevailing environmental conditions (Wingfield & Romero 1999). Chronically elevated and prolonged high levels of corticosterone can be physiologically harmful to individuals, affecting immune function, growth, reproduction and survival (Wingfield 1994). Thus, elevated circulating corticosterone may indicate that an animal is stressed even if obvious behavioural changes cannot be detected (Eilam *et al.* 1999; Walker *et al.* 2005). Conversely, not every behavioural response to the occurrence of a human leads to a physiological stress response (Müller *et al.* 2006). Animals in a critical body condition (e.g. starving) may show only weak behavioural reaction to humans (e.g. flight distances; Stillmann & Goss-Custard 2002; Beale & Monaghan 2004a).

Studies investigating effects of human disturbance on animals usually focus either on behavioural (Stalmaster & Kaiser 2004) or on physiological responses to disturbance (Wasser *et al.* 1997) and, therefore, can be misleading (see above). Studies using simultaneously both behavioural and physiological measures of disturbance are rare (but see Walker *et al.* 2005; Walker *et al.* 2006), and only few studies investigated the effect of winter tourism on free-ranging animals (but see Creel *et al.* 2002; Watson & Moss 2004).

In this study, we investigated both habitat use as a behavioural response and faecal glucocorticoid levels as a physiological response of capercaillie to ski tourism. Many populations of capercaillie in Europe became extinct or declined rapidly within the last decades (Storch 2000a; Pollo *et al.* 2005). Capercaillie are considered a disturbance-sensitive species, and it has been shown that capercaillie abandoned lek sites (Labigand & Munier 1989) or declined in numbers (Brenot *et al.* 1996) after skiing area expansion. Therefore, human disturbance ranges among the main-potential causes of population decline in addition to habitat deterioration and forest fragmentation (Storch 2000b). Human induced stress in winter could be especially harmful, because the energy budget in winter is tight due to the limitation to feed only on low-quality conifer needles in winter (Klaus *et al.* 1989). Therefore, extra energy expenditure such as repeated flushing could lead to negative energy budgets. Information about the susceptibility of capercaillie to human disturbance is urgently needed for effective management plans and conservation strategies for capercaillie in or near winter tourism areas. This is especially important as most capercaillie habitats in Central Europe are located in areas with human recreation activity.

Methods

STUDY AREA AND STUDY SPECIES

We conducted the study in the forest-dominated mountain range of the Southern Black Forest in south-western Germany (47°51'N, 07°58'E). The study area (2812 ha) consisted of capercaillie habitat in 2 plots (A and B; Fig. 1–2) with elevations ranging from 900 –1400 m. They are separated by a steep valley of 5 km width with unsuitable habitat, and contain of several sub-plots (A–H) separated by topography. Plots were demarcated by elevation (>900 m), paved roads or pastures without trees. The hilltops and valley bottoms are only gently sloped or flat, covered with patchy forests and interspersed with extensively used pastures. The steeper slopes are completely forested. Forests are managed by forestry and intensively used by various recreation activities, and dominated by nutrient-rich forest stands containing Norway spruce *Picea abies (*49%), European silver fir *Abies alba* (19%) and common beech *Fagus sylvatica* (*22%*; Suchant *et al.* 2003). Winter climate is temperate with high precipitation (2000 mm/year) and mean daily temperatures (November–January) of -1.3°C (DWD Deutscher Wetterdienst). The area is snow-covered from December–April, with a snow depth of 0.5–3m. Recreation activities in the snow-free season are mainly hiking and mountain biking, and in winter cross-country skiing, downhill skiing (only in plot A, Fig. 1) and hiking. Except for a tourist lodge in sub-plot C (Fig. 1) and an intensively used outdoor sport facility in sub-plot H (Fig. 2), no year-round used buildings, paved roads or car parks exist within the study area. The density of unpaved forest roads mainly used for hiking and mountain biking is high (26m/ha). Compared to ski tourism, snow-shoeing was relatively rare. Backcountry- and free-riding skiing was frequent in the down-hill skiing area between ski-runs in the upper part of sub-plot C (Fig. 1). The intensively used cross-country ski-tracks with up to 1000 visitors a day (R. Roth, pers. comm.) are confined to prepared forest roads or are situated in un-forested areas outside the study area. Intensive ski tourism starts with the first snow fall (between early and late December) when the snow depth allows the preparation of cross-country ski-tracks and ski-runs. Before the ski season starts, only few hiking tourists visit the study area. The ski season ends with the snow melt in early spring (March/April).

In the entire Black Forest (7 000 km^2), capercaillie declined rapidly during the last decades and persist in isolated fragments on 510 km^2 with about 500 individuals (Braunisch & Suchant 2006). The study area was located within the core population of the Southern Black Forest, and is currently inhabited by about 60 individuals.

RADIO TRACKING AND HABITAT USE

Seven capercaillie males and 8 females were caught in nets in September–October in the years 2003 and 2004. Birds were equipped with a 25–69 g backpack radio transmitter (<4% of body mass; Titley Electronics Ltd, Ballina, Australia, Model GPI; Atstrack Advanced Telemetry Systems Inc, Isanti, Minnesota, Model A1540; and Microwave Telemetry Inc, Columbia, Maryland, Model PTT-100). Birds were located between 1 November and 31 March in 3 subsequent winters 2003/04–05/06 by 'homing in' (Kenward 2001) using a 3-element hand-held antenna. To avoid disturbance, most bearings were taken from forest roads or ski-tracks <1 km distance. Because the spatial activity of capercaillie in winter is low (Gjerde *et al.* 1985; Storch 1993), canopy closure is relatively open (many leafless

deciduous trees), and the access to most forests easy (many ski-tracks), all bearings were accurate and could be included in the analyses.

We defined 2 time periods, because recreation intensity vastly changed over the course of the winter. The period 'before the ski season' started at 1 November (early winter with leafless deciduous trees, capercaillie already using their winter habitats) and lasted until the first heavy snow fall when the ski season started. The period 'during the ski season' started with this first day of the ski season until 31 March as the end of the study period, because after that the space use of capercaillie changes due to early lekking behaviour. Since 1 male (#1) and 2 females (#1, #3) were predated during the winter and because 1 female (#5) established its winter home range late in winter, the number of individuals for the spatial analyses before the ski season started was 12, and 10 for analyses during the ski season (Table 1). We included all birds in the analysis with > 22 radio locations per study period (before or during the ski season). The time between 2 consecutive radio locations ranged between 4 hours and 25 days (mean = 1.88 days).

Home ranges were determined by the minimum convex polygon method (MCP; GIS software ArcView 3.2), separately for the 2 time periods before and during the ski season, and encompassing all capercaillie radio locations per individual (Table 1). The surface of the study area and home ranges were calculated by excluding un-forested areas and very steep slopes >40° as unsuitable habitat (no radio locations of capercaillie in such habitats).

We treated the intensity of recreation and thus the potential of human disturbance as a component of habitat quality. We defined 3 classes of recreation intensity. All forested areas with no human presence during the winter (e.g. inaccessible areas or away from any ski-tracks) were digitized as REC1 (low recreation intensity). All regularly used tourism infrastructure in forests such as ski-tracks, ski-lifts, ski-runs, hiking trails, roads, the tourist lodge and other sport facilities with a buffer of 50m were digitized as REC3 (high recreation intensity, see Fig. 1–2). A previous study in this study area revealed that 90% of all observed capercaillie flushed within 50m between bird and an off-trail hiker (n = 752, Thiel *et al.* 2007a). All the remainder of capercaillie habitat was classified as area with moderate recreation intensity (REC2). As a second variable of habitat quality, we used the steepness of the slope with 2 categories (SLO1 = 0–10°, SLO2 = 10–40°, based on 50 x 50 m grid cells; Braunisch & Suchant 2007). It has been shown that capercaillie prefer flat snow-rich mountain ridges and hilltops, and avoid steep slopes (Graf *et al.* 2005; Graf *et al.* 2006; Klaus *et al.* 1989).

Since the spatial pattern and intensity of recreation changed markedly before and during the ski season, the recreation intensity classes were defined separately for the 2 periods. The classes of recreation intensity REC2 and REC3 are therefore a relative measure for recreation intensity per period, and do not reflect the same intensities in both periods. Whereas REC3 during the ski season accounts e.g. for ski-tracks used by several hundred tourists per day, REC3 comprises forest roads with only a few hikers. REC1 was always associated with low recreation intensity.

SAMPLING OF DROPPINGS

All droppings were sampled from 1 November–31 March in the 2 winters 2003/04 and 2004/05 and in the same study area as described above. We located radio-equipped capercaillie every 3–5 weeks to sample their fresh droppings. In addition, fresh droppings from capercaillie without radios were

searched by walking along contour lines crossing forests, and visually searching for droppings on the surface of the snow (see Thiel *et al.* 2007b). We determined the sex of the capercaillie from the size of the intestinal droppings, i.e. dropping diameter of males >10 mm, and those of females <8 mm (K. Bollmann, unpubl. data). Since home ranges of capercaillie in winter are quite small, the droppings were spatially clumped. We only sampled fresh droppings and considered droppings from the same sex within a circle of 300 m surrounding a dropping (28.3 ha) as originating from the same individual. Therefore, we assigned each dropping of an individual without a transmitter to a potential individual, as an approach to prevent pseudo-replication in statistical analyses. Since we only sampled fresh droppings and we knew at the time of sampling where the radio-equipped birds were located, we could avoid to unintentionally sample droppings from radio-equipped birds. We sampled 5–15 individual droppings at each location (=1 dropping sample).

For each dropping sample, we determined the following predictor variables for the analyses (see below): RADIO (without or with radio transmitter), INDIVIDUAL (potential individual for birds without a radio or individual radio-equipped birds), SEX (male or female), SEASON (before or during) and minimum daily temperature TEMPMIN from the next meteorological station (DWD Deutscher Wetterdienst), because ambient temperature is known to affect energy metabolism, food intake, dropping production and therefore steroid measurements (Goymann *et al.* 2006). Furthermore, we determined the type of droppings DROPTYPE in 3 categories (night roost droppings, foraging droppings, and droppings excreted during walking or day roosting on the ground, see definitions in Thiel *et al.* 2007b). Caecal droppings were not sampled due to their different composition of micro-organisms affecting enzymatic steroid metabolism (Klasing 2005). Each dropping sample was assigned to a slope category SLOPE (SLO1, SLO2) and a recreation intensity class RECREATION (REC1–3) by GIS software ArcGIS 9.1. In total, we obtained 106 dropping samples from 14 radio-equipped individuals (n = 2–19 per individual, from all individuals except female # 1, Table 1). The 290 droppings from birds without a radio were assigned to 53 potential individuals (n = 1–14 per individual) according to the method described above. All samples were stored at -23°C until analysis. We had not to be aware of diet composition as a determinant of glucocorticoid metabolite concentration (Goymann 2005), since capercaillie in winter feed exclusively on conifer needles (Storch *et al.* 1991), in the southern Black Forest especially on Norway spruce needles (Lieser 1996). Other important factors affecting steroid metabolism such as season of the year, vast changes in energy requirements or reproductive status (see Millspaugh & Washburn 2004) were not relevant since we only sampled droppings in winter.

CORTICOSTERONE METABOLITE MEASUREMENTS

Since the fecal concentration of glucocorticoids reflexes the level in the plasma, measuring fecal corticosterone is an ideal non-invasive method to biomonitor the endocrine status of shy and rare free-living species. Levels of glucocorticoids are therefore independent of the sampling procedure, thus being feedback-free (Goymann 2005). Glucocorticoids are metabolized in various organs; droppings contain therefore a mixture of several different glucocorticoid metabolites with a wide range of polarities. Because glucocorticoid metabolism is often species- and sometimes even sex-specific, a careful physiological and technical validation of protocols and methods to measure faecal

glucocorticoids for the investigated species is necessary (Möstl *et al.* 2005; Touma *et al.* 2003). We evaluated an enzyme immunoassay to reliably measure corticosterone metabolite concentrations (CMC) in capercaillie droppings (see Thiel *et al.* 2005). CMC in capercaillie droppings remain stable for at least 21 days as long as the ambient temperature is < +9°C (Thiel *et al.* 2005), which was the case throughout our study period, and time of day do not influence CMC.

Since we were interested in measuring potential long-term effects of recreation intensity on the basal level of corticosterone, we wanted to eliminate potential short-term effects of other stressors such as predator appearance. Moreover, due to differences in corticosterone metabolite concentrations between droppings (Baltic, 2005), probably caused by the pulsed excretion of corticosterone by the bile (Klasing, pers. comm.), we collected and homogenized the 5–15 droppings per individual and sampling location to obtain a mean concentration of these metabolites over a longer time span.

STATISTICAL ANALYSES

We used mixed models to test whether individual home range size differs with the number of bearings per individual (BEARINGS) or with season (SEASON) with the method of Residual Maximum Likelihood Analysis REML (Patterson & Thompson 1971). INDIVUDAL was included as a random effect; BEARINGS, SEASON and its interaction term as fixed effects.

We combined the categories of the 2 habitat classifications (REC and SLO) resulting in 6 habitat types: REC1SLO1, REC1SLO2, REC2SLO1, REC2SLO2, REC3SLO1, REC3SLO2. To test whether habitat use of capercaillie is influenced by recreation intensity, we applied compositional analysis (Aebischer *et al.* 1993), using an Excel macro (Smith 2005) for 2 types of analyses:

First, we compared the composition of the 6 habitat types in the home ranges with the availability of the habitat types in the entire study area. This was done for both seasons separately and tested whether the home ranges of capercaillie were preferentially located in areas of particular habitat types. Then, we tested whether habitat types used before the ski season which later (during the ski season) became heavily affected by recreation, were avoided during the ski season. For this test of potential habitat shifting, we assigned home ranges before the ski season to the recreation intensity classes of the ski season for all 9 individuals of which we had enough data from both periods. Then, we compared this habitat composition of home ranges with that during the ski season, by adding the variable SEASON as an independent variable in the Wilk's log-ratio matrices, and analysed these matrices by a MANOVA (Aebischer *et al.* 1993). In addition, to test whether home range composition of the recreation classes REC1–3 differed between sexes, we added the variable SEX as an independent variable in the Wilk's log-ratio matrices, and analysed these matrices by a MANOVA (Aebischer *et al.* 1993).

Secondly, we compared habitat use, as revealed by the composition of the habitat types from the telemetry locations, within each home range with availability (habitat composition of the corresponding home ranges). For both seasons separately, we tested whether capercaillie preferred or avoided certain habitat types within their home ranges. The tests for potential habitat shifting and sex differences were performed as described above.

Following (Aebischer *et al.* 1993), we substituted missing values by a small proportion (0.001%) for available but unused habitat types. 1000 iterations for randomizations were used. For each compositional analysis of capercaillie habitat use, Wilk's lambda (λ) and randomized *P* values were reported.

We used REML to identify factors affecting CMC. Data of years were pooled, and data from birds with and without radios were analyzed in the same model, since we tested for any effects of wearing a radio transmitter by the variable RADIO. The model contained all 6 predictor variables as fixed effects and the variable INDIVIDUAL as a random effect. Furthermore, we included the 3 interaction terms SEX*SEASON, SEX*RECREATION and SEASON*RECREATION, because we expected them to be biologically relevant. Non-significant interaction terms were omitted from the final model. We used GenStat for Windows version 7.3 (Payne 2003) for this analysis.

Results

HABITAT USE

Before the tart of the ski season, capercaillie were more evenly distributed and used a higher proportion of the study area compared with the situation during the ski season when capercaillie locations were more aggregated in certain areas (Fig. 1–2, sub-plots A, B, D, H). Twenty-three % of all locations (n=107) were in areas which later, during the ski season, were highly used by recreation (REC3). Forty-nine % (n=42) of all locations during the ski season in areas with high recreation intensity (REC3) occurred on days when the number of skiers was low or even zero, mostly due to bad weather conditions. However, the availability of such days with low recreation activity when we radio-tracked birds was only 25% (n=29), thus capercaillie mostly used REC3 areas when recreationists were absent. The area around the tourist lodge (Fig. 1; sub-plot C), the ski-runs (Fig. 1; upper part of sub-plot C) and an intensively used outdoor sport facility (Fig. 2; sub-plot H) were used before the ski season started, but not any more, or only rarely, during the ski season (Fig. 1–2). In contrast to ski-runs, areas with cross-country ski-tracks only were used before and during the ski season.

The REML-analysis showed that only the variable SEASON significantly affected home range size and was not influenced by the number of bearings (Wald χ_1^2 -probability = 0.006). Home ranges (MCP) before the ski season were larger than during the ski season for all individuals except for male # 5 (Table 1), but the location of the home ranges did not change between the two periods. Seventy-five ± 5.3 % (mean ± SE, n=9) of the home range area during the ski season were already part of the home range area before the ski season. Although home range size was smaller during the ski season, capercaillie did not markedly dislocate or change their home range with the start of the ski season, except for male # 1. Before the ski season started, this male used forests with ski-runs and ski-lifts. With the beginning of the ski season it dislocated to an area in 2700 m distance with moderate recreation intensity REC2 (cross-country skiing area) by crossing a valley of 1500m width. After 3 weeks he returned close to the previous location but in a forest with low recreation intensity (REC1), where he got predated by a red fox *Vulpes vulpes*.

In a next step, we analysed at the individual level, whether the composition of the 6 habitat types in the home ranges differed from the habitat composition of the entire study area. Before the ski

season, capercaillie home range composition did not differ from the composition of the study area (Wilk's λ = 0.618, χ^2 = 0.539, *randomized P* = 5.777; Fig. 3a). During the ski season, habitat composition of capercaillie home ranges differed slightly from availability in the study area (Wilk's λ = 0.138, χ^2 = 19.841, *randomized P* = 0.045), but without significant differences between habitat types (Fig. 3b). Capercaillie used slightly more areas before the ski season that later became REC3 areas, than during the ski season, but this test for a potential habitat shifting was not significant (MANOVA, λ =0.432, *F* = 2.888, *P* = 0.066). Before and during the ski season, home ranges of males randomly consisted of the 3 recreation classes REC1–3 (Wilk's λ = 0.389, χ^2 = 5.665, *randomized P* = 0.185, and Wilk's λ = 0.329, χ^2 = 5.553, *randomized P* = 0.234, respectively). However, females significantly preferred areas with high recreation intensity REC3 before the ski season (Wilk's λ = 0.304, χ^2 = 7.115, *randomized P* = 0.037) over REC2 and REC1, but there was no preference of a certain recreation intensity class during the ski season (Wilk's λ = 0.645, χ^2 = 2.196, *randomized P* = 0.621). Habitat use did not significantly differ between males and females before (MANOVA, λ =0.665, *F* = 2.265, *P* = 0.160) or during the ski season (MANOVA, λ =0.812, *F* = 0.812, *P* = 0.482).

On a smaller scale, we analysed whether habitat use, as revealed by the locations within home ranges, differed from the habitat composition of the corresponding individual home ranges. Before the ski season, capercaillie preferred areas with moderate recreation intensity REC2 to REC1 and REC3b (Wilk's λ = 0.252, χ^2 = 16.539, *randomized P* = 0.018; Fig. 4a). During the ski season, capercaillie significantly preferred undisturbed areas REC1d to highly disturbed areas REC3 (Wilk's λ = 0.1522, χ^2 = 18.824, *randomized P* = 0.046; Fig. 4b). Capercaillie used slightly more areas before the ski season that later became REC3 areas, than during the ski season (Figure 4b), but this test for a potential habitat shifting was not significant (MANOVA, λ =0.204, *F* = 3.895, *P* = 0.081). Capercaillie males and females did not reveal a significant habitat preference for one of the 3 habitat types REC1–3, whether before Wilk's λ = 0.554, χ^2 = 3.547, *randomized P* = 0.129 for males, Wilk's λ = 0.331; χ^2 = 5.976, *randomized P* = 0.075 for females) nor during the ski season (Wilk's λ = 0.208, χ^2 = 7.846, *randomized P* = 0.196 for males; and Wilk's λ = 0.303, χ^2 = 5.976, *randomized P* = 0.223 for females). Habitat use did not significantly differ between males and females before (MANOVA, λ =0.720, F = 1.552, P = 0.269) or during the ski season (MANOVA, λ =0.882, F = 0.403, P = 0.685).

STRESS HORMONE ANALYSES

Five out of 7 variables included in the multivariate analysis (SEX, SEASON, TEMPMIN, DROPTYPE and RECREATION) significantly contributed to explain variation in CMC (Table 2). Males (predicted mean ± SE: 45.0 ± 2.36 ng/g droppings) exhibited generally higher CMC than females (37.7 ± 2.34 ng/g droppings; Fig. 5a, b). CMC before the ski season (34.6 ± 3.12 ng/g droppings) was significantly lower than during the ski season (48.6 ± 1.86 ng/g droppings; Fig. 5a, b). CMC increased with decreasing minimum daily temperatures (Table 2). CMC from night roost droppings (41.3 ± 1.41 ng/g droppings) were lower than from those excreted during foraging (44.0 ± 1.54 ng/g dropping) or excreted during walking or day roosting on the ground (49.5 ± 2.54 ng/g droppings). CMC of capercaillie in both periods were lower in areas with low (REC1) than moderate (REC2) recreation intensity (effect size: 9.8, Fig. 5a, b). CMC of capercaillie in areas with REC2 did not differ from those with high recreation intensity REC3 (effect size: 8.4; Fig. 5a, b). CMC of Capercaillie with or without a

radio transmitter did not differ. Habitat slope did not contribute to explain variation in CMC. None of the 2-way-interaction terms was significant.

Analyzing only the 106 droppings from the 14 individually known radio-tracked individuals with the same predictor variables (except for RADIO), the same variables were significant except for SEX (P = 0.456) and DROPTYPE (P = 0.466). RECREATION had by far the largest impact of all variables (P = 0.002, effect size: 13.2 for REC2 and 11.0 for REC3).

Radio-tracked capercaillie with individual home ranges containing <20% area with high recreation intensity during the ski season (REC3) had lower CMC values than those with home ranges containing >20% REC3 area, except for the 2 females # 4 and # 6 (Fig. 6).

Discussion

This study shows that ski tourism affects habitat use and evokes physiological stress in capercaillie. Other studies demonstrated a decrease in capercaillie abundance following the construction of ski-facilities (Drillon 1989; Labigand & Munier 1989; Brenot *et al.* 1996), but this is the first study investigating simultaneously spatial behavioural and physiological responses of the same capercaillie individuals to human winter recreation. In addition, this study is one of the first studies investigating the impact of ski tourism on grouse. Our results demonstrate that results from a radio-tracking study at a small spatial scale can differ from those on a large spatial scale. Congruently, results from a behavioural study on the same individuals can be contradictory to a physiological study. Therefore, we recommend to use several methods at different spatial scales to evaluate the impact of human recreation on animals.

HABITAT USE

Capercaillie home range location within the study area was not influenced by winter recreation intensity, neither before nor during the ski season. The majority of capercaillie home ranges in our study area overlapped with highly used cross-country ski-tracks, ski-runs or hiking trails. In addition, capercaillie did not change the location of their home ranges with the beginning of the ski season, and we did not observe movements out of heavily disturbed areas except for one male.

However, capercaillie were affected by winter recreation at a fine spatial scale within the home range. (1) During the ski season, capercaillie strongly preferred areas with low recreation intensity, (2) avoided areas around the intensively used tourist lodge, ski-runs, and the outdoor sport facility in sub-plot H, (3) their locations were spatially clumped in areas with low winter recreation intensity, which was not the case before the ski season. (4) During the ski season, capercaillie used areas with ski facilities (REC3) mainly when there were no or only a few tourists. Low frequency of tourists on trails before the ski season had no noticeable effect on capercaillie habitat use.

The general decrease in home range size and the increased aggregation of capercaillie locations in certain areas with the start of the ski season could also be related to the concomitant increase of the snow depth. With high snow cover, foraging on ground vegetation becomes impossible and birds are restricted to feed on conifer needles as the only winter food (Storch *et al.* 1991). Since conifer needles are a low-quality forage (Moss & Hansson 1980), this change in food availability and quality could cause capercaillie to reduce energy expenditure by a reduction in their spatial activity, as

already postulated by Gjerde & Wegge (1987) and Thiel *et al.*(2007b). However, the preference of capercaillie during the ski season for areas with low recreation intensity within their home ranges is unlikely to be caused by snow depth or food availability, because capercaillie in our study area mainly feed on the superabundant and spatially evenly distributed Norway spruce (Lieser 1996).

In this study, we did not investigate direct behavioural responses such as alerting or flushing to winter recreationists and we do not know whether the long-distance displacement of a single capercaille male with the start of the ski season is a common phenomenon. However, Thiel *et al.* (2007*a*) showed that capercaillie had larger flushing distances in areas with high than with low winter recreation intensity. Repeated flights lead to extra energy expenditures and are then higher in areas with high human recreation intensity. The potential of negative fitness consequences in winter due to behavioural responses to skiers is therefore given, which was shown by Morrison *et al.* (1995) in elk *Cervus elaphus nelsoni*: increased winter recreation activity did not only decrease the number elks visits in disturbed areas. Energy expenditure moving away from cross-country skiers represented approximately 5.5 % of an estimated average daily energy expenditure for elk in winter and exceeded the normal level of daily energy expenditure for movement (Cassirer 1992). Beside energy expenditure, human disturbance can also affect immune competence: common wall lizards *Podarcis muralis* in summer inhabiting areas with high tourism levels had lower body mass and higher parasite infection than those in low-level tourism areas, and lizards with poorer body condition had a lower cell mediated immune response (Amo *et al.* 2006).

STRESS HORMONE ANALYSES

For capercaillie droppings from radio-equipped individuals and for those without radios, faecal corticosterone metabolite concentration CMC was significantly higher in areas with moderate or high recreation intensity than in those with low recreation intensity. This was the case for males and females, and before and during the ski season. Even droppings on low frequented hiking trails before the start of the ski season (REC3) showed higher CMC compared to areas away from such disturbance sources. This result is in contrast to our findings on habitat use, where a low frequency of tourists on trails before the ski season had no noticeable effect on capercaillie habitat use within home ranges. Similar to our findings, faecal glucocorticoid levels in wolves *Canis lupus* were higher in areas of heavy snowmobile use, and day-to-day variation in faecal glucocorticoid levels in elk *Cervus elaphus* paralleled variation in the number of snowmobiles (Creel *et al.* 2002).

Our results demonstrate that the presence of capercaillie in skiing areas does not justify the conclusion that capercaillie are not susceptible to human disturbance. Although we do not know which corticosterone basal level entails negative fitness consequences in capercaillie, studies in other species showed that the potential for negative consequences of a disturbance-induced elevated glucocorticoid level is high. Carolina chickadees *Poecile carolinensis* from disturbed (logged) forests with higher faecal corticosterone levels had a lower body mass than birds from undisturbed forests (Lucas *et al.* 2006). Juvenile hoatzins *Opisthocomus hoazin* living at ecotourist-exposed sites had a lower body mass, a higher mortality, and showed a stronger increase of corticosterone to experimental stress compared to individuals at undisturbed sites (Müllner *et al.* 2004).

The reason for the higher glucocorticoid level of males compared to females is unclear. Several studies have found a pronounced gender difference of baseline and stress-induced levels of glucocorticoids (Goymann 2005; Touma & Palme 2005). A possible reason could be a gender-specific capacity of steroid-binding globulines with differential affinities to corticosterones in the plasma (Breuner & Orchinik 2002). Another explanation would be that this gender-difference of CMC indeed reflects differences in plasma corticosterone levels, and males are more stressed than females. Such a potentially higher susceptibility of males to human recreation activities was already postulated by Thiel *et al.* (2007a): (1) capercaillie flushing distances of males as a response to an off-trail hiker were larger than for females. (2) Capercaillie flew at larger distances in areas with high intensity of winter tourism or hunting pressure than in undisturbed areas, and this difference was more pronounced for males than for females. Interestingly, a positive correlation of human activity with faecal glucocorticoid concentration and flushing distance was also found in free-living Pampas deer stags *Ozotoceros bezoarticus bezoarticus* (Pereira *et al.* 2006).

The strong effect of season on CMC (higher CMC during the ski season than before) could be caused by either the higher recreation activity during the ski season or by environmental changes imposed by snow depth. With the increase of snow depth, capercaillie change their forage from energy-rich and easy digestible bilberries *Vaccinium myrtillus* on the forest ground to low-quality conifer needles in trees. However, the effect of season on CMC is unlikely to be caused by temperature, since we obtained the same significance of season even when we corrected for temperature by changing the order of the predictor variables in the REML-analysis. Fortunately, we could control or avoid other important factors affecting CMC such as age and storage of samples (Millspaugh *et al.* 2003; Washburn & Millspaugh 2002), sex (Touma *et al.* 2003), temperature (Goymann *et al.* 2006), season of the year (Hiebert *et al.* 2000), diet (Goymann 2005), and habitat quality (Suorsa *et al.* 2003).

THE IMPORTANCE OF REFUGES

Two main reasons could explain why the effect of winter recreation on capercaillie habitat use was spatial scale-dependent, and why capercaillie used skiing areas despite the possible negative consequences of an elevated corticosterone level.

First, capercaillie probably use skiing areas only if refuges without human access are available within their home ranges. Adjacent to disturbance sources, the topography may create such refuges as for humans inaccessible forest patches with a visual and acoustic shield against disturbances (such as in sub-plot A and E). In addition, on-trail disturbances such as recreationists on cross-country tracks are tolerated better than noisy disturbance sources and those frequently used by many people with a great area of influence (tourist lodge, shooting stand, down-hill ski-runs) or off-trail disturbances. Off-trail disturbances are unpredictable and sporadic, and are difficult for animals to get used to (Miller *et al.* 2001).

Secondly, habitat requirements of capercaillie and skiers are similar. Winter tourism in the Southern Black Forest is restricted to the highest snow-rich elevations, mostly dominated by flat and gently sloped coniferous forests with low tree stem density. These forests are also the last high-quality capercaillie habitats in this region. Braunisch & Suchant (2007) showed that the degree of snow cover

best explains capercaillie winter distribution in the Black Forest. Therefore, despite the possible negative effects of inhabiting skiing areas, capercaillie may not be able to move away from disturbed areas because they probably cannot find a suitable habitat nearby. Or frequent or long-distance movements as a response to disturbance may be too costly or too risky, because this would decrease body condition and increase predation risk.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

We conclude that areas with frequent winter recreation activities are sub-optimal capercaillie habitats. This is indicated by the effects of winter recreation on habitat use and physiological stress as shown in our study, and by studies on mortality and reproduction in other grouse species: in skiing areas, wires of ski-lifts caused mortal collisions in black grouse (Miquet 1990) and rock ptarmigan *Lagopus mutus* (Watson & Moss 2004), and reproductive success of rock ptarmigan was low due to a high general predator abundance (Watson & Moss 2004). We therefore recommend to avoid the creation of new skiing areas, and not to expand existing ones, in or adjacent to capercaillie habitats. In areas where capercaillie habitat overlaps with winter recreation activities, management plans should ensure interspersed forest patches without human access as refuges, and that off-trail activities should be prevented in capercaillie core areas. Regulations for tourists to stay on trail and the dislocation or closure of trails and tracks in capercaillie core areas can decrease the area of disturbance influence, and thus increase suitable capercaillie habitat. Hazel grouse *Bonasa bonasia*, black grouse and other species would probably also benefit from such management activities, because they share similar habitat requirements with capercaillie and are probably affected similarly by winter recreation (Baltic 2005).

Acknowledgments

We thank Dölf Egenter, Samuel Ehrenbold, Judith Ehrlacher, Christoph Grütter, Jonas Kleyer, Christof Elmiger, Ruedi Meier, Peter Nyffeler, Uli Querner, Matthias Ritschard, Tobias Roth, Thomas Sattler, Andreas Schmidt, and Conny Thiel-Egenter for their assiduous fieldwork. We are especially grateful to the foresters Wolfgang Ebser and Claudio Röhmer-Litzmann, who supported this study with valuable help and access in the field. We thank Peter Berthold, Wolfgang Fiedler and Rudi Suchant for their great support to conduct the radio-tracking study. Marc Kéry supported us with statistical analyses, and Beat Naef-Daenzer with radio-tracking technique. For his helpful comments to this manuscript, we thank Christian Marti, Philip Tipping and Niklaus Zbinden. D. Thiel was financially supported by the International Council for Game and Wildlife Conservation CIC, and the Janggen-Pöhn-Foundation. All catching and radio-tracking of capercaillie were carried out under the permit of the Regierungspräsidium Freiburg, Baden-Württemberg (Freiburg; No 0-9213.21, höhere Naturschutzbehörde).

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Table 1. *Number of bearings collected before and during the ski season for 7 radio-tracked capercaillie males and 8 females, and the size of their home ranges (Minimum convex polygon; in ha) before and during the ski season for birds with more than 22 bearings per period. Individuals with < 23 bearings (in brackets) were not included in statistical analyses.*

	Individual	Number of bearings		Home range (MCP; in ha)	
		before	during	before	during
1	Male # 1	27	(5)	59	–
2	Male # 2	23	25	141	22
3	Male # 3	30	31	185	137
4	Male # 4	41	63	171	125
5	Male # 5	49	95	208	245
6	Male # 6	51	102	548	219
7	Male # 7	(17)	0	–	–
8	Female # 1	29	0	179	–
9	Female # 2	39	26	79	66
10	Female # 3	45	(21)	130	–
11	Female # 4	45	67	134	58
12	Female # 5	(9)	69	–	128
13	Female # 6	43	65	118	71
14	Female # 7	52	96	367	104
15	Female # 8	(6)	(14)	–	–

Table 2. *Dependence of the concentration of corticosterone metabolites CMC in capercaillie droppings (n = 396) on various predictor variables analyzed in a multivariate linear REML-model with the individual bird INDIVIDUAL as the random effect. Effects ± SE were calculated considering a reference value of zero for RADIO(no), SEX(male), SEASON(before), DROPTYPE(night roosting), SLOPE(0–10°) and RECREATION(low).*

Independent variables	Effect ± SE	Wald statistics	df	*P*
Constant	31.491 ± 4.65			
RADIO (yes)	2.860 ± 3.01	0.23	1	0.63
SEX(female)	-7.815 ± 2.59	11.37	1	<0.001
SEASON(during)	13.609 ± 3.25	10.66	1	0.001
TEMPMIN	-0.569 ± 0.23	9.5	1	0.002
DROPTYPE		7.25	2	0.027
Foraging	-1.022 ± 2.68			
day roosting/walking	5.297 ± 2.68			
SLOPE(10–40°)	-3.089 ± 2.14	3.18	1	0.074
RECREATION		17.91	2	<0.001
moderate	9.957 ± 2.88			
high	8.894 ± 2.88			

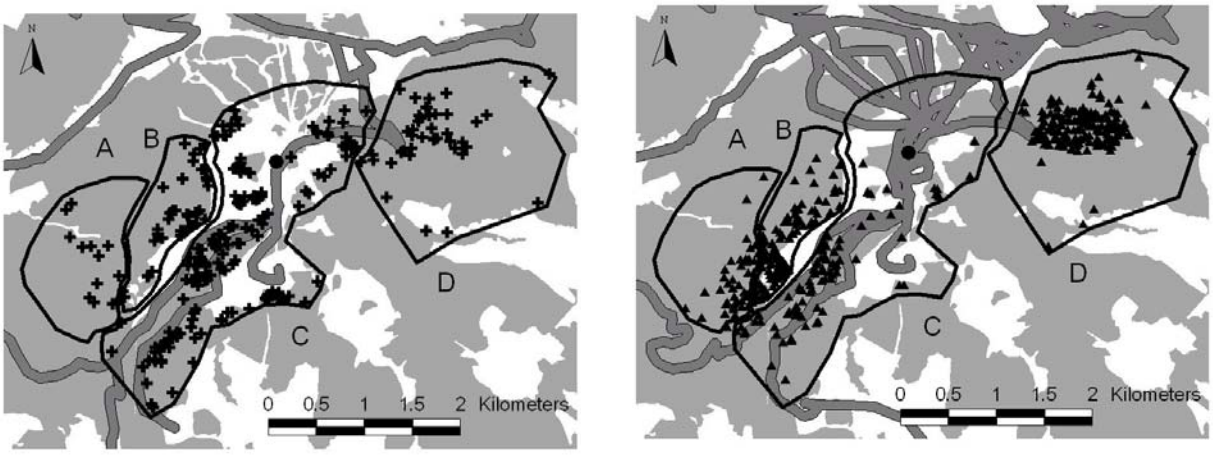

Figure 1. *Locations of 1 male and 4 females in study plot B in the 3 winters 2003/04–2005/06 in the Southern Black Forest before the ski season (a; crosses) and during the ski season (b; triangles). High recreation intensity areas REC3 are marked in dark grey, and contained intensively used hiking trails and cross-country tracks (sub-plots C) and ski-runs (upper part of sub-plot C) with a buffer of 50 m. Forests are marked in light grey, open meadows in white. The black dot indicates the location of an intensively used tourist lodge. Some outlying locations are not shown.*

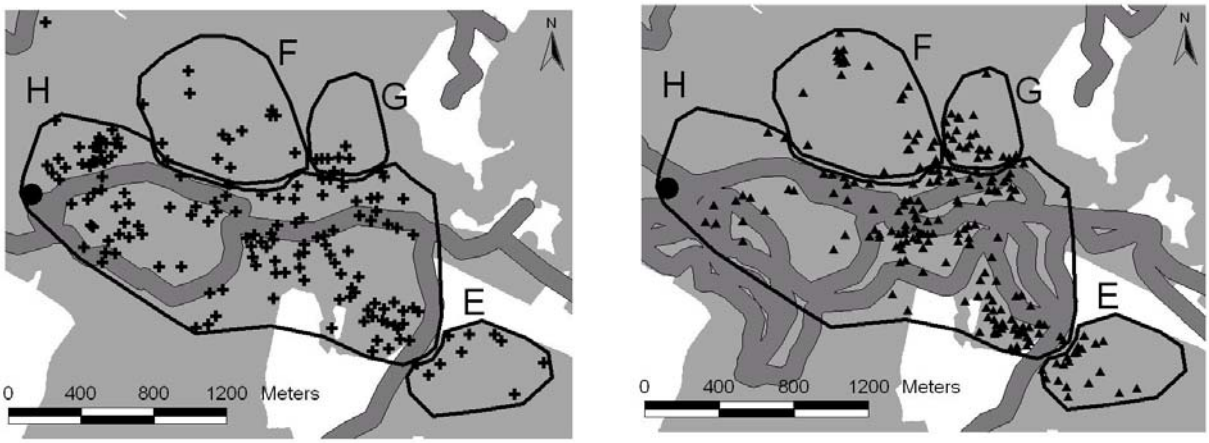

Figure 2. *Locations of 5 radio-tracked capercaillie males and 3 females in the 3 winters 2003/04–2005/06 in study plot A in the Southern Black Forest before the ski season (a; crosses) and during the ski season (b; triangles). High recreation intensity areas REC3 are marked in dark grey, and contained intensively used hiking trails and cross-country tracks (sub-plots H) with a buffer of 50 m. Forests are marked in light grey, open meadows in white. The black dot indicates the location of an intensively used outdoor sport facility. Some outlying locations are not shown.*

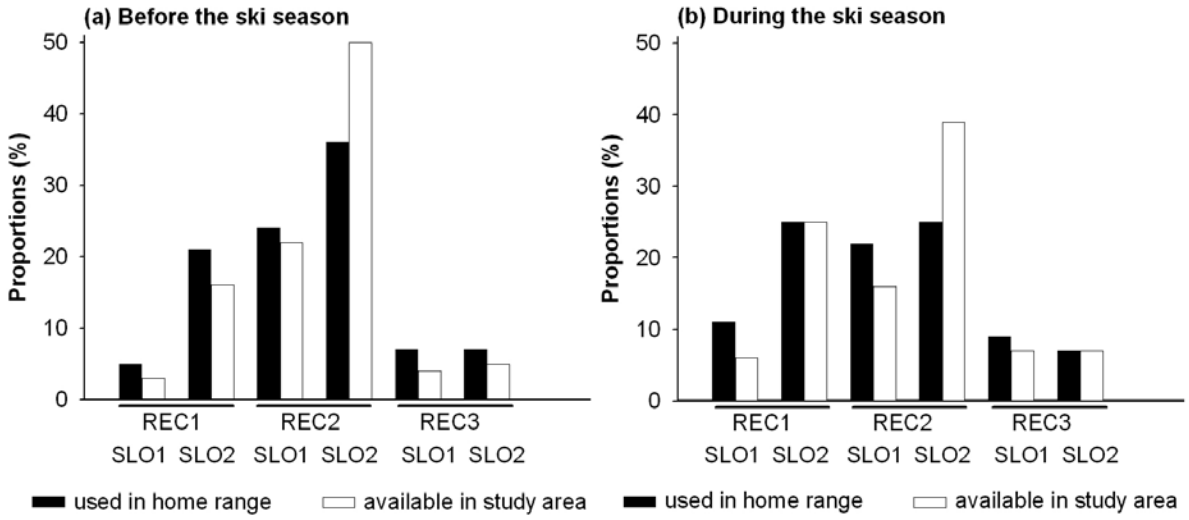

Figure 3. *Proportions of 6 habitat types of recreation intensity classes (REC1 = low recreation intensity, REC2 = moderate recreation intensity, REC3 = high recreation intensity) and habitat slope categories (SLO1 = 0–10°, SLO2 = 10–40°) of capercaillie winter home ranges compared to the availability in the entire study area (a) before and (b) during the ski season. There were no significant differences between availability and use of the 6 habitat types.*

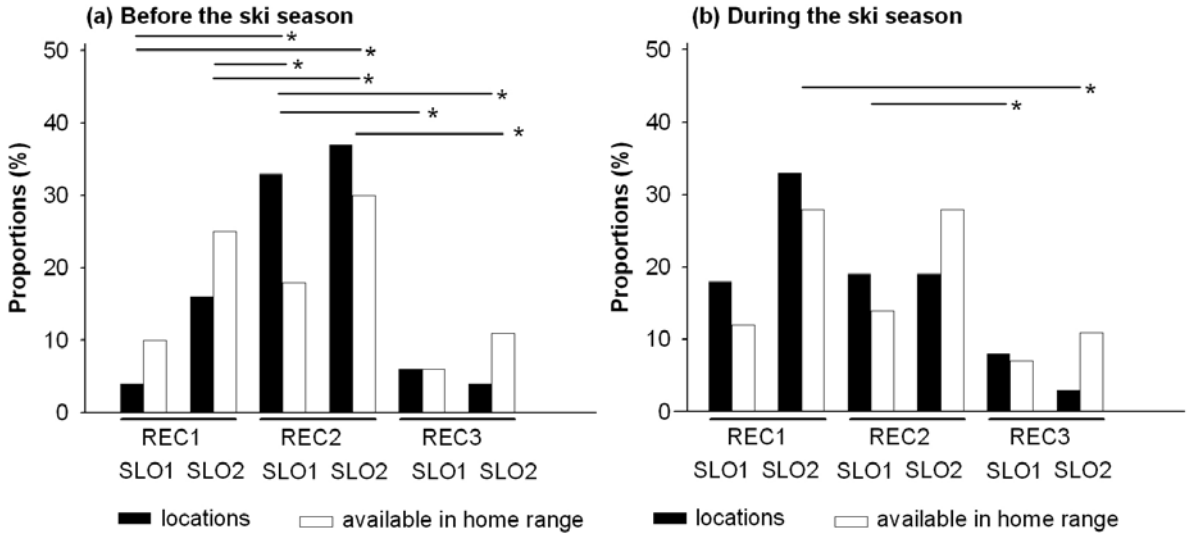

Figure 4. *Proportion of the 6 habitat types (see Fig. 3 for detailed explanations) used within home ranges (locations) compared to the composition of their individual home ranges (a) before and (b) during the ski season. * (P<0.05, compositional analysis) indicate significant differences between habitat types connected by a line.*

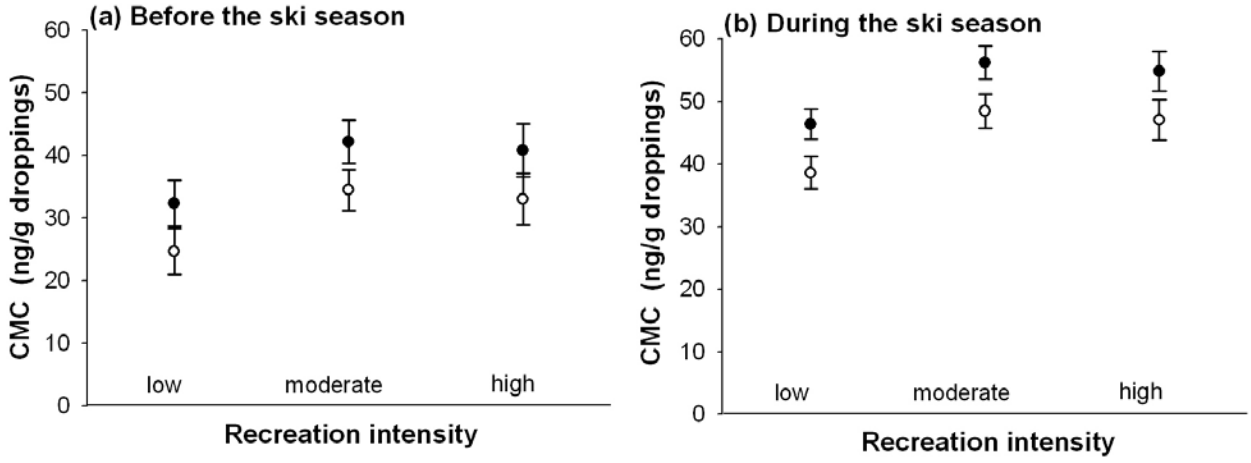

Figure 5. *Predicted means (± SE) of the REML-analysis of corticosterone metabolite concentration (CMC) in capercaillie droppings (n=396) of males (filled circles) and of females (open circles) for 3 recreation intensity classes (a) before and (b) during the ski season. The recreation intensity levels 'moderate' and 'high' are a relative measure per period, and do not reflect the same intensities in both periods.*

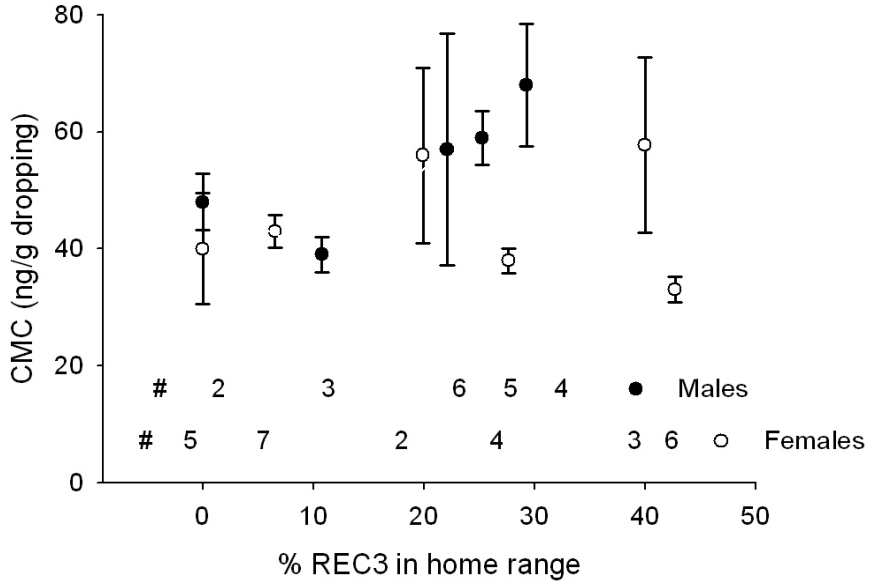

Figure 6. *Observed means (± SE) of corticosterone metabolite concentration (CMC) in droppings of 5 males (filled circles) and of 6 females (open circles) showing their home range composition (in %) of highly disturbed area (REC3) during the ski season.*

Paper V

Evidence for physiological stress in capercaillie *Tetrao urogallus* due to human winter recreation

To be submitted as:

Dominik Thiel[1, 2], Susanne Jenni-Eiermann[1], Rupert Palme[3], and Lukas Jenni[1]. Evidence for an endocrinological stress response to winter recreation in capercaillie *Tetrao urogallus.*

[1]Swiss Ornithological Institute, CH-6204 Sempach, Switzerland

[2]Institute of Environmental Sciences, University of Zurich, Winterthurerstrasse 190, CH-8057 Zurich, Switzerland

[3]Institute of Biochemistry, Department of Natural Sciences, University of Veterinary Medicine, Veterinärplatz 1, A-1210 Vienna, Austria

Abstract

The capercaillie *Tetrao urogallus*, a forest grouse with specific habitat requirements, suffered from rapid population declines during the last decades over much of its distribution range. In Central Europe, many capercaillie populations inhabit areas with intensive human recreation activities, which may contribute to this decline. However, little is known about its susceptibility to human disturbance. This study examined whether human recreation in winter evokes physiological stress in capercaillie. During two winters, we sampled 1130 capercaillie droppings in the Black Forest/Germany, the Swiss Alps and the Swiss Jura of populations exposed to various human pressure and measure faecal corticosterone metabolite concentration. Capercaillie in mountain forests dominated by Norway spruce *Picea abies* showed markedly increased stress hormone levels with decreasing distance to the next disturbance source. However, this physiological response to human recreation was absent in habitats where stress hormone levels were constantly high. This study shows that capercaillie physiologically respond to winter recreation with an increase in stress hormone level under certain environmental conditions. We suggest that capercaillie are especially sensitive to winter recreation, because any factors affecting the fine-tuned physiological and behavioural adaptations of capercaillie to survive under harsh winter conditions may lead to harmful fitness costs. We recommend to prevent the access of winter recreationists in undisturbed capercaillie winter habitats, and retain capercaillie core areas apart from areas with frequent recreation activities.

Introduction

The capercaillie (*Tetrao urogallus*) is the largest grouse worldwide and inhabits boreal forests within its large and continuous distribution range from Scandinavia to eastern Siberia (Klaus *et al.*, 1989). Most of the remaining populations in Central and Western Europe nowadays are confined to high elevation coniferous mountain forests. Populations are often small (<200 individuals), and inhabit strongly fragmented habitat patches (Storch, 2000a; Storch, 2000b). The shrinkage of the distribution range was paralleled by a decline in population sizes since several decades. This led to the listing of the capercaillie in many national red-data books in Central and Western Europe as threatened or in danger of extinction (Storch, 2000a; Storch *et al.*, 2006). Several reasons at different spatial scales have been suggested to cause these strong population declines including habitat loss and degradation, climate change and predation. In addition, increasing human recreation activities in capercaillie habitats are supposed to contribute to this population decline (Storch, 2000a). While the capercaillie is a well-studied species, knowledge about the susceptibility to human disturbance is mainly lacking. Some case studies documented local population declines or even extinctions after an increase in human outdoor activities (Drillon, 1989; Labigand & Munier, 1989; Brenot *et al.*, 1996). Especially recreation activities in winter are of great conservation concern, since the energy budget in winter is tight, the rate of energy intake limited and, thus, the potential for negative fitness consequences high. For example, additional energy expenditure could be caused by frequent escape flights of capercaillie in ski areas, since flushing distances of capercaillie as a response to an off-trail hiker in habitats with high recreation intensity are larger than those with moderate or low recreation intensities (Thiel *et al.*, 2007a).

A promising way to evaluate the susceptibility of free-ranging animals to human recreation is to measure the endocrine status, which reflects a physiological stress response of individuals to stressors. Glucocorticoids (corticosterone in birds) are released into the blood after the activation of the hypothalamo-pituitary-adrenal axis (Sapolsky *et al.,* 2000). Stress hormone levels are of great fitness relevance, since chronically elevated levels affect growth, body condition, immune-function, reproduction and survival (Wingfield *et al.*, 1997). Since capercaillie in Central Europe are rare, endangered, and difficult to catch, collecting plasma sample for stress hormone analyses is not feasible. Therefore, measuring corticosterone metabolites in faeces is a suitable method for working with free-ranging and rare animals. Faecal glucocorticoid analyses have become increasingly popular, since they have many advantages over plasma analyses (Touma & Palme, 2005). The sampling procedure does not influence the endocrine profile and, thus, is feedback-free. It does not conflict with animal welfare, and faecal sampling can be applied on a large scale involving many populations and habitat types. Furthermore, faecal analyses provide an integrated measure of steroid levels over a longer period of time rather than a point measure of circulating levels at the time of blood sampling (Goymann, 2005). Despite the many promising benefits of this method, a careful validation of sample storage, extraction procedure, and immunoassay is crucial (Touma & Palme, 2005), since steroid metabolism is species and sometimes even gender-specific (Goymann, 2005). In a previous study, we validated an enzyme immunoassay to measure corticosterone metabolite concentrations in capercaillie droppings (Thiel *et al.*, 2005b).

Human recreation activities in capercaillie habitats are most extensive in winter, and winter is the most energetically demanding season of the year for many species. Therefore, we investigated the endocrine stress response of capercaillie to human winter recreation activities. We conducted an extensive sampling of capercaillie droppings in populations in Germany and Switzerland on a large area in various types of mountain forests and winter recreation intensities to asses the faecal stress hormone level. We hypothesized that capercaillie close to potential disturbance sources or in habitats with high winter recreation intensity would show higher levels of corticosterone metabolites than those far away from human presence.

Methods

We sampled fresh capercaillie droppings in winter core habitats during two winters (1 November–31 March) in 2003–04 and 2004–05 in 3 study areas with temperate winter climate in Central Europe (Fig. 1): Southern Black Forest in south-western Germany (47°51'N, 07°58'E), Western Swiss Jura (46°33'N, 6 °15'E) and in the Swiss Alps (46°45'N, 9 °04'E). In the Black Forest study area, we sampled in 3 study sites totalling 11 km^2 between 900–1400 m. Forests consisted mainly of Norway spruce *Picea abies* (49%), European silver fir *Abies alba* (19%) and common beech *Fagus sylvatica* (22%; Suchant *et al.*, 2003). In the Swiss Jura, droppings originated from 5 sites with an area totalling 4 km^2 at elevations ranging from 1300–1500 m. Forests were dominated by Norway spruce (73%), European silver fir (12%) and common beech (10%; U. Ulmer, pers. comm.). Pines were absent in the Black Forest and in the Swiss Jura study areas. In the Swiss Alps, we searched droppings in 57 sites totalling 51 km^2 with a large variety of different forest types and elevations ranging from 1300–2200 m. Tree composition varied from pure to mixed coniferous forests with different tree species dominating (*Picea abies*, *Abies alba, Pinus sylvestris, Pinus mugo*, *Pinus cembra*, *Larix decidua*). Proportions of deciduous trees (common beech, sycamore maple *Acer pseudoplatanus*) were <10% in all the sites of the Swiss Alps. Inter-site distances were > 1 km in all study areas, and sites were regarded as independent of each other, since capercaillie space use in winter is very confined (Gjerde *et al.*, 1985; Storch, 1993). Snow covered the forest ground on all sampling days in all sites, and the majority of mean daily temperatures (November–January) in all sites was <0°C.

Winter recreation in all study areas consisted of ski tourism (cross-country skiing, back-country skiing and down-hill skiing on ski-runs or off-trail), snow-shoeing, hiking, sledding and dog-sledding, but without year-round used buildings or villages. In some study sites only a single recreation activity was conducted, in other sites several, or none. The recreation intensity ranged from sites without any human presence over the entire winter to heavily used skiing areas with several hundred skiers a day. Other human activity than winter recreation was almost absent during our study period, except for some selective tree harvesting in early winter.

Estimated population size in the Black Forest study area exceeded 60 capercaillie (Braunisch & Suchant 2006), was about 56 in the Swiss Jura study site (S. Sachot, pers. comm.), at least 350 in all Swiss Alp sites combined (K. Bollmann and P. Mollet, pers. comm.).

Each site was visited twice during the winter: once in early winter before the start of the ski season (November–December), and once in mid- or late winter during the ski season (January–March). Droppings were searched on the snow surface by walking along contour lines in capercaillie

core areas. Capercaillie sex was determined based on the size of the intestinal droppings (males >10 mm, females <8 mm; K. Bollmann, unpubl. data). We considered droppings from the same sex within a 300-m radius around the dropping (28.3 ha) as originating from the same individual, since winter home range in winter and capercaillie density are small, and we only sampled fresh droppings. Thus, each dropping was assigned to a potential individual (INDIVIDUAL) to avoid pseudo-replication. We sampled 5–15 individual droppings on each location, which we called a dropping sample. For each dropping we determined sex (SEX: male or female), season (SEASON: before or during the ski season), dominating forest type (FOREST: *Picea-Abies* forest or *Pinus-Larix* forest), minimum daily temperature from the next meteorological station corrected for the elevation by 0.6°C per 100 m (TEMPMIN; ©MeteoSchweiz), date (DATE; transformed Julian date by numbering each day from 1 November to 31 March), type of dropping (DROPTYPE in 3 levels: excreted during 'night roosting' in trees, excreted during 'foraging' in trees, and those excreted on the ground while 'day roosting or walking'; see methods in Thiel *et al.*, 2007b), and the distance (in m) to the next frequently used disturbance source (DISTURBANCE; ski-run, ski-track, ski-lift, hiking trail, road, a.s.o.). These disturbance sources were digitised in GIS (ArcGIS 9.1), and the smallest distance from each dropping to the next disturbance source was calculated. SEASON was determined for each study site separately, depending on local conditions. The period 'before the ski season' lasted usually from 1 November to Christmas holiday, i.e. before the ski facilities (ski-lifts, cable cars, a.s.o.) started their service, with frozen forest ground and usually small depth of snow. The period 'during the ski season' lasted from Christmas holiday or the beginning of the ski season until the end of our study period. *Picea-Abies* forests contained either almost only *Picea abies* or were intermixed with small proportions of *Abies alba*. *Pinus-Larix* forests contained substantial amounts of different *Pinus* species (see above), some intermixed with small proportions of *Larix deciduas*.

Since the aim was to measure an average basal level of faecal corticosterone metabolites for a given bird and not its short-term variation, the 5–15 droppings collected at anyone location were pooled and homogenized before lyophilisation, extraction and analysis (Thiel *et al.*, 2005b). Corticosterone metabolite concentration CMC in the droppings was measured as described by Thiel *et al.* (2005b). This previous study confirmed that CMC can be reliably measured if droppings are fresh and ambient temperatures are < +9°C, which is fulfilled in winter. However, due to differences in corticosterone metabolite concentrations between droppings (Baltic, 2005), probably caused by the pulsed excretion of corticosterone by the bile (Klasing, pers. comm.), we collected and homogenized the 5–15 droppings per individual and sampling location to obtain a mean concentration of these metabolites over a longer time span.

We used mixed model REML (Residual Maximum Likelihood Analysis; Patterson & Thompson, 1971) to identify factors affecting CMC with INDIVIDUAL as a random effect and all the 7 predictor variables as fixed effects. Years were pooled. The 3 continuous predictor variables TEMPMIN, DATE and DISTURBANCE were also included in the model as squared variables to test for non-linearity. In a first step, we included all possible 2-way and three 3-way interaction terms, which we expected a priori to be of biological relevance. Non-significant interaction terms were omitted from the final model. We used GenStat for Windows version 7.3 (Payne, 2003) for this analysis.

Results

In total, we sampled and analysed 1130 droppings: 290 droppings in the Black Forest, 101 in the Swiss Jura and 739 in the Swiss Alps. Mean concentration of corticosterone metabolites was 49 ng/g droppings ± 0.6 SE (range: 6–179 ng/g droppings; 90% percentile: 74 ng/g droppings). Of the 7 variables examined in the multivariate analysis, all variables were significantly related to CMC (Table 1). Males had generally higher CMC than females (Table 1), but this pattern was dependent on the sampling date. Whereas CMC of males increased from November to March, the corresponding values of females decreased during this period (Fig. 2). Since the effects of the other significant predictor variables on CMC differed with forest type, we present the further results for the two forest types separately.

Picea-Abies forests

Season significantly affected CMC in combination with forest type and type of dropping (Table 1). CMC in droppings excreted during night roosting and foraging was lower before than during the ski season (Fig. 3a–d), whereas the corresponding value for droppings excreted during walking or day roosting on the ground did not differ among season (Fig. 3e–f). CMC increased with decreasing distance to the next disturbance source. This was especially marked when birds were on the ground while walking or day roosting and at high minimum daily temperatures. The effect of minimum daily temperature was dependent on forest type, type of dropping and distance to the next disturbance source (Table 1). CMC strongly increased with decreasing minimum daily temperature in droppings far away from disturbances, whereas this temperature-dependence was much less pronounced close to disturbances, where CMC was generally high (Fig. 3a–f). Therefore, CMC in droppings under low minimum daily temperatures far away from disturbances had similarly high levels as CMC in droppings close to disturbances at any temperatures. This pattern was especially pronounced in droppings excreted during walking or day roosting on the ground: CMC markedly increased with decreasing temperatures far away from disturbances, but was almost independent on temperatures close to disturbances (Fig. 3e–f).

Pinus-Larix forests

CMC in droppings found in *Pinus-Larix* forests was generally higher than those found in *Picea-Abies* forests (Fig. 3a–f; 4a–f). As in *Picea-Abies* forests, season significantly affected CMC in combination with type of dropping (Table 1). CMC was higher before than during the ski season in droppings excreted during night roosting (Fig. 4a–b), whereas this pattern was reversed in droppings excreted during walking or day roosting on the ground with higher CMC during than before the ski season (Fig. 4e–f). CMC did not vary with season in droppings excreted during foraging. The effect of minimum daily temperature varied with type of dropping and distance to the next disturbance source (Table 1). Similar to the pattern in *Picea-Abies* forests, CMC generally increased with decreasing minimum daily temperature in droppings excreted during night roosting and foraging (Fig. 4a–d), but this negative correlation was much stronger in *Pinus-Larix* forests than in *Picea-Abies* forests. However, CMC increased with increasing minimum daily temperature in droppings excreted during day roosting and walking, especially close to disturbance sources (Fig. 4e–f), thus opposite to the corresponding

pattern in *Picea-Abies* forests (Fig. 3e–f). CMC did not markedly vary with distance to the next disturbance source (Fig. 4a–f), and was therefore different to the situation in *Picea-Abies* forests.

When we ran our model with recreation as a categorical variable with 3 classes of recreation intensity (low, moderate, high) based on our field observations and local expert knowledge, we obtained almost the same result. The effect of recreation intensity was highly dependent on forest type. CMC increased from low to high recreation intensity in *Picea-Abies* forests (predicted means ± SE: 39 ± 2.1; 44 ± 1.5; 49 ± 1.8), but with no substantial differences among the recreation intensities in *Pinus-Larix* forests (52 ± 2.0, 51 ± 1.8, 55 ± 3.3).

Discussion

Although some case studies have examined capercaillie abundance before and after the construction of ski facilities, this is one of the first studies investigating an individual and physiological response of capercaillie to recreation activity, and of grouse to winter recreation in general. Our results suggest that winter recreation evokes physiological stress in capercaillie based on the following reasons: (1) Independent of sex, season and type of dropping, stress hormone levels increased with decreasing distance to the next disturbance source in *Picea-Abies* forests. (2) The strong effect of temperature on CMC found in *Picea-Abies* forests decreased with increasing closeness to the next disturbance source. This temperature effect even disappeared during the ski season when birds were close to disturbance sources while walking or day roosting on the ground. (3) The highest stress hormone levels in *Picea-Abies* forests were found in capercaillie droppings close to disturbance sources together with low temperatures. (4) Although the variable DISTURBANCE was included as the last predictor variable in our model, CMC was significantly affected by disturbance in *Picea-Abies* forests. Results were very similar when using distance to the next disturbance source or an expert categorisation (low, moderate, high) as a measure of recreation intensity, although we sampled in many capercaillie populations subjected to various types of recreation activities and intensities. Therefore, recreation in winter is an important determinant of stress hormone level in capercaillie in addition to other environmental variables such as temperature. Similar results were found in droppings from radio-tracked capercaillie in the Black Forest (Thiel et al. in prep.): CMC increased with increasing winter recreation intensity.

According to Beale & Monaghan (2004), free-ranging animals perceive humans as real predators and respond by the occurrence of a recreationist with an antipredatory behaviour. A physiological response to the occurrence of a predator or recreationist is the activation of the hypothalamo-pituitary-adrenal axis with the release of glucocorticoids into the blood as a mechanism to adjust the behaviour and the physiology of animals to prevailing environmental conditions (Wingfield & Romero, 1999). Thereby, the animals become physiologically prepared to overcome a dangerous situation for example by fleeing. However, chronically elevated and prolonged high levels of corticosterone can be physiologically damaging with negative fitness consequences (Wingfield, 1994). The increased stress hormone levels in capercaillie close to disturbance sources in *Picea-Abies* forests have therefore a high potential to negatively affect capercaillie fitness. A reduced fitness due to human-induced elevated stress hormone levels was shown by other authors. Carolina chickadees *Poecile carolinensis* in disturbed forests had higher faecal corticosterone levels and lower

body mass than birds from undisturbed forests (Lucas *et al.* 2006). Juvenile hoatzins *Opisthocomus hoazin* living at ecotourist-exposed sites had a lower body mass, a higher mortality, and showed a stronger increase of corticosterone to experimental stress compared to individuals at undisturbed sites (Müllner *et al.* 2004).

In the context of an antipredatory behaviour, we can understand why capercaillie in *Picea-Abies* forests and during the ski season walking or day roosting on the ground showed high CMC, almost independent on temperatures. Capercaillie on the ground are more conspicuous than in trees and the risk is high to get predated by abundant and ground-hunting predators such as red fox *Vulpes vulpes (Wegge et al., 1987).* Therefore, the birds are probably more careful and feel less safe on the ground than in trees, especially in winter when camouflaging vegetation on the forest ground is rare. Thiel *et al.* (2007a) found similar results: capercaillie males on the ground in areas with high hunting pressure had longer flushing distances than those perching in trees. Similarly, ungulates in mountain areas showed shorter alert distances to the presence of recreationists when they were situated below the animals than above them (Taylor & Knight, 2003). These results demonstrate that the location of recreationists in relation to animals affects the behavioural and the physiological stress response.

Sex differences

There are two possible reasons why stress hormone levels increased from early to late winter in males, but decreased slightly in females. Either there is a gender and season-specific capacity of corticosterone binding globulines (CBG; Breuner & Orchinik, 2002; Romero *et al.*, 2006), or it is due to the gender-specific start of lekking behaviour for the upcoming lekking season in spring. In contrast to females, males start with lekking behaviour already in winter during warm ambient temperatures without the presence of females, and before regularly visiting lek sites (Klaus *et al.*, 1989; Thiel *et al.*, 2005a). Although we did not sample droppings from capercaillie with lekking activity, sexual preparation of males for the upcoming lekking season could cause an increase of CMC. The slight decrease of CMC in females in the corresponding time could be due to the tighter energy budget of females. Females with a smaller body size have a higher 'lower critical temperature', and higher mass-specific energy requirements and heat loss in relation to body weight, than males (Rintamäki *et al.*, 1984). An increase in circulating corticosterone induces catabolic metabolism, which could lead to a critical body condition, and impair a successful reproduction in spring. Several other studies indicate that females are either less susceptible to human disturbance or their tighter energy budget does not allow a response to stressors without negative fitness consequences. Flushing distances of females as a response to an off-trail hiker are shorter and the increase in flushing distances with human recreation intensities is less pronounced than that of males (Thiel *et al.*, 2007a).

Environmental conditions

Minimum daily temperature strongly affected CMC in capercaillie droppings. CMC increased with decreasing temperatures. This is most likely an adaptation to harsh environmental conditions. In winter, when bilberry *Vaccinium myrtillus* and other important and nutrient-rich food sources on the ground are inaccessible, capercaillie only feed on conifer needles. Conifer needles are a superabundant but low-quality food with high contents of cellulose and secondary plant compounds

(Andreev, 1988; Lindén, 1984). Capercaillie are well-adapted to this food, and decompose and digest cellulose with the aid of bacteria in the large caeca during a long-lasting process (Moss & Hansson, 1980). As a result, the rate of food- and energy intake in winter is strongly limited. Therefore, capercaillie reduce their spatial and daily activity in winter to reduce energy expenditure (Gjerde & Wegge, 1987; Storch, 1995). However, below the thermoneutral zone of –3°C for males and +9°C for females (Rintamäki *et al.*, 1984), metabolic rate needs to be increased. Corticosterone is well-known to accelerate metabolism, and is suggested to initiate food-searching behaviour during periods of food deprivation (Astheimer *et al.*, 1992). Elevated corticosterone levels also serve to mobilize energy stores via protein catabolism (Harvey *et al.*, 1984). Therefore, the increased corticosterone levels under decreasing ambient temperatures are most probably an adaptation to harsh environmental conditions. Huber *et al.* (2003) found the same effect of minimum ambient temperature and snow on faecal glucocorticoid excretion in red deer *Cervus elaphus*.

Interestingly, the effect of ambient temperature on CMC was dependent on the distance to the next disturbance source. Far away from disturbances, CMC strongly increased with decreasing temperature (except for CMC in droppings excreted on the ground in *Pinus-Larix* forests). Close to disturbance sources, CMC was generally higher and less influenced by temperature in *Picea-Abies* forests, than far away from disturbances. It seems that a capacity boarder of CMC exists, which can either be reached by a natural stress response (low temperatures) or a stress response induced by anthropogenic disturbances.

The reason why CMC in *Pinus-Larix* forests was generally higher than in *Picea-Abies* forests could be due to a higher abundance of predators such as pine martens *Martes martes*. Because capercaillie prefer pine trees *Pinus spp.* over *Picea abies* for night roosting (Thiel *et al.*, 2007b) and feeding (Schroth *et al.*, 2005), it is unlikely that tree species explain the high CMC in *Pinus-Larix* forests. Why capercaillie in *Pinus-Larix* forests do hardly increase CMC as a response to human disturbances is unclear. This pattern could be caused by the large standard errors of the predicted means for *Pinus-Larix* forests, thus, being less reliable than those for *Picea-Abies* forests. This is due to the fact that we found only few droppings in *Pinus-Larix* forests close to disturbance sources and during warm temperatures. In *Picea-Abies* forests, droppings were quite well distributed among the various levels of predictor variables, and therefore predictions more reliable.

Conclusions

The physiological and behavioural adaptations allow capercaillie to survive harsh winter conditions with low temperatures, high snow depth and limited energy intake for several months per year. Any factors affecting this fine-tuned physiological and behavioural balance and any additional factors affecting the tight energy budget may lead to negative fitness consequences. This study suggests a physiological stress response to human recreation with potentially harmful consequences. Thiel et al. (in prep.) demonstrated that capercaillie preferred undisturbed areas and avoided highly disturbed areas within their home ranges. Longer flushing distances of capercaillie in areas with high compared to low recreation intensity could lead to high energy costs (Thiel *et al.*, 2007a). Moreover, wires and cables of ski-lifts can cause mortal collisions for grouse (Miquet, 1990). Therefore, we believe, that capercaillie are especially sensitive to winter recreation, and the risk for negative effects is high. The

access of winter recreationists in undisturbed capercaillie winter habitats should therefore be prevented. Recreation activities should be kept apart from capercaillie winter core areas, especially during the physiologically most demanding winter days with temperatures far below 0°C.

Acknowledgments

We thank Batist Bischoff, Dölf Egenter, Judith Ehrlacher, Ruedi Meier, Pierre Mollet, Peter Nyffeler, Emmanuel Rey, Franz Rudmann, Tobias Roth, Thomas Sattler, Conny Thiel-Egenter, and Thomas Wicki and numerous game keepers for their assiduous fieldwork by collecting capercaillie droppings under harsh environmental conditions in mountain forests. We are especially grateful to Kurt Bollmann, Wolfgang Ebser, Ruedi Hess, Hannes Jenny, Claudio Röhmer-Litzmann, and Sébastien Sachot, who supported this study with valuable help or access in the field. For their helpful comments to this manuscript, we thank Philip Tipping. Dominik Thiel was financially supported by the International Council for Game and Wildlife Conservation CIC, and the Janggen-Pöhn-Foundation.

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Table 1. *Dependence of the concentration of corticosterone metabolites CMC in capercaillie droppings (n = 1130) on various predictor variables analyzed in a multivariate linear REML-model with the individual bird INDIVIDUAL as the random effect. Effects ± SE were calculated considering a reference value of zero for SEX(male), SEASON(before), FOREST(Picea-Abies) and DROPTYPE(night roosting).*

Independent variables	Effect ± SE	Wald statistics	df	*P*
Constant	42.080 ± 3.93			
Main effects				
SEX(female)	-7.001 ± 1.33	40	1	<0.001
SEASON(during)	6.186 ± 4.33	5	1	0.021
TEMPMIN	-0.509 ± 0.30	40	1	<0.001
$TEMPMIN^2$	-0.001 ± 0.00	2	1	0.119
FOREST(*Pinus-Larix*)	26.960 ± 33.25	15	1	<0.001
DATE	-0.118 ± 0.133	2	1	0.169
$DATE^2$	0.001 ± 0.00	3		0.077
DROPTYPE		6	2	0.064
foraging	-1.036 ± 4.87			
day roosting/walking	6.921 ± 4.60			
DISTURBANCE	-0.015 ± 0.01	1	1	0.354
$DISTURBANCE^2$	0.000 ± 0.00	8	1	0.005
Interaction terms				
SEX(female)×DATE	0.191 ± 0.18	23	1	<0.001
SEX(female)×$DATE^2$	-0.002 ± 0.00	4		0.035
SEASON(during)×DROPTYPE	-	8	2	0.021
SEASON(during)×FOREST(*Pinus-Larix*)	-13.651 ± 5.50	4	1	0.037
TEMPMIN×DROPTYPE	-	13	2	0.002
TEMPMIN×DISTURBANCE	-0.000 ± 0.00	4	1	0.043
FOREST(Pinus-Larix)×DROPTYPE	-	8	2	0.017
FOREST(Pinus-Larix)×DISTURBANCE	0.012 ± 0.01	5	1	0.022
TEMPMIN×DROPTYPE×FOREST(Pinus-Larix)	-	10	3	0.015
$TEMPMIN^2$×DROPTYPE×FOREST(Pinus-Larix)	-	17	5	0.005
SEASON(during)×FOREST(Pinus-Larix)×DROPTYPE	-	8	2	0.018

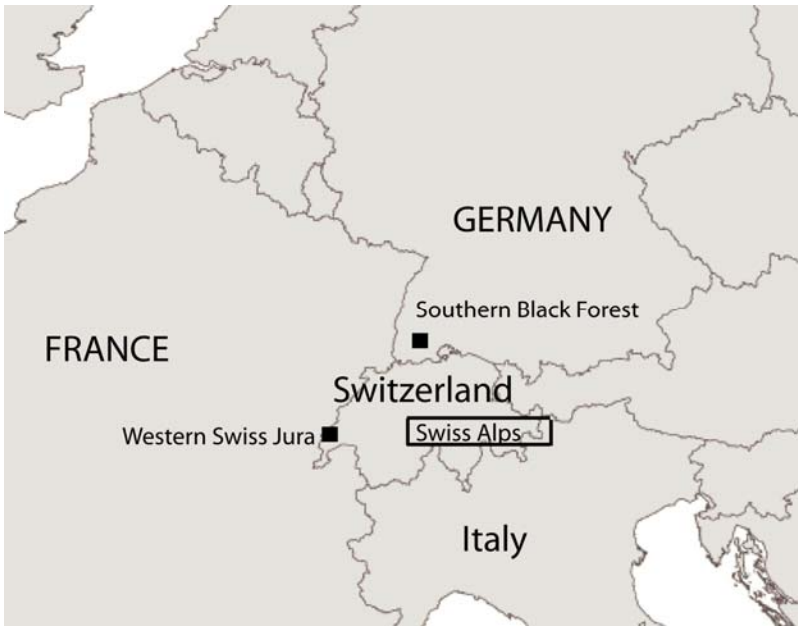

Figure 1. *Locations of the 3 study areas Southern Black Forest in southwestern Germany, Western Swiss Jura, and Swiss Alps, where we collected 1130 droppings from capercaillie in two winter 2003–04 and 2004–05 to analyse stress hormone levels (© Institute of Cartography ETH Zürich).*

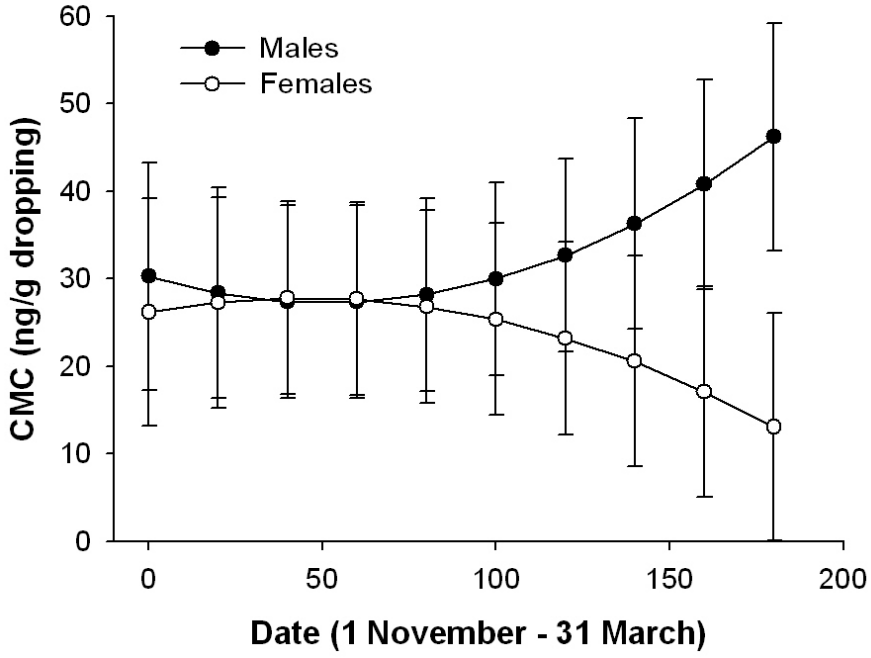

Figure 2. *Predicted means (± SE) of the REML-analysis of corticosterone metabolite concentration (CMC) in capercaillie droppings (n=1130) for males (circles) and females (crosses) among the study period (DATE = transformed Julian date by numbering each day from 1 November to 31 March).*

Figure 3.

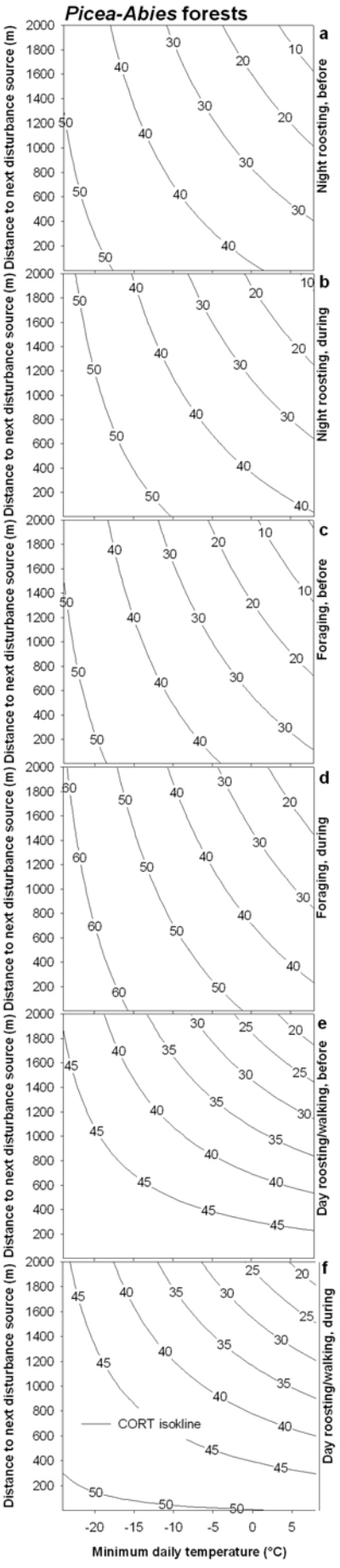

Figure 4.

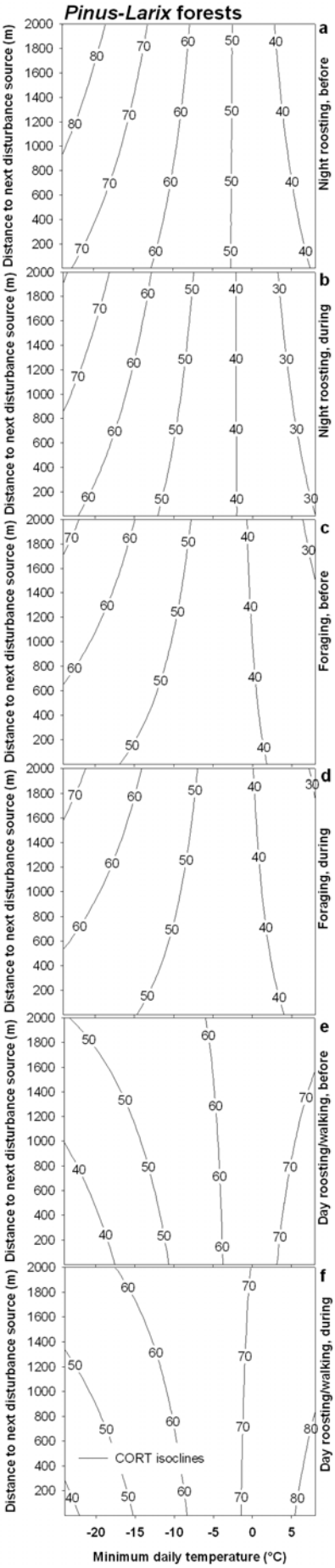

Figure 3. *Contour line plots showing the isoclines of the predicted means of the corticosterone metabolite concentration (CMC) sampled in Picea-Abies forests in relation to minimum daily temperature (°C) and to distance to the next disturbance source (DISTURBANCE; in m) for droppings excreted during (a–b) night roosting in trees, (c–d) foraging in trees, and (e–f) walking or day roosting on the ground for the period 'before' (a, c, e) and 'during' the ski season (b, d, f).*

Figure 4. *Contour line plots showing the isoclines of the predicted means of the corticosterone metabolite concentration (CMC) sampled in Pinus-Larix forests in relation to minimum daily temperature (°C) and to distance to the next disturbance source (DISTURBANCE, in m) for droppings excreted during (a–b) night roosting in trees, (c–d) foraging in trees, and (e–f) walking or day roosting on the ground for the period 'before' (a, c, e) and 'during' the ski season (b, d, f).*

Synthesis

The main aim of this thesis was to investigate how capercaillie respond to winter recreation in order to determine the susceptibility of capercaillie to human disturbance. To reach this goal, we first validated a method to measure stress hormone metabolites in capercaillie droppings as a physiological indicator of stress (paper I), second investigated certain aspects of capercaillie habitat selection at the individual level (paper II), and third analyzed the behavioral (paper III and IV) and physiological (paper IV and V) response of capercaillie to winter recreation. In this synthesis chapter, I discuss issues of methodology, behavior, physiology and conservation.

Methodological aspects

The capercaillie is a rare and shy forest grouse living in a habitat where the detection and direct observation of free-ranging animals is strongly limited. In addition, various invasive methods to investigate stress hormones of animals (a. o. blood samples) cannot be applied because of the conservation status of capercaillie. Therefore we had to choose methods, which do not conflict with animal welfare, and deliver a sufficient sample size for statistically powerful analyses.

The non-invasive method of measuring fecal corticosterone metabolites fulfilled these requirements (paper I). Moreover, this method was cost-effective and after some training also relatively easy to handle. However, a careful validation of the method to investigate the metabolism and excretion pattern of these metabolites on the study species is necessary to reliably assess adrenocortical activity. This validation is not that simple and straight forward, but is necessary for designing an adequate field protocol. The results of this validation confirmed that the applied enzyme immunoassay reliably measured fecal corticosterone metabolites. We also demonstrated that fecal corticosterone metabolite concentrations were stable over several days under winter conditions, and that stress hormone levels did not vary with daytime as found in other species (Breuner, Wingfield & Romero 1999).

In paper II, we investigated the selection of winter night roosts as an important aspect of winter ecology in capercaillie. We searched for night roosts while collecting capercaillie droppings for analyzes in paper IV and V, and therefore we limited our visits to capercaillie core areas. We determined night roosts by the simultaneous presence of intestinal and cecal droppings. Thereby, we avoided searching night roosts by radio-tracking the birds during the night, and could enlarge the sample size for individuals without radios. Because of distinct sex-specific dropping sizes, we were also able to address sex differences in night roost selection. We compared available and used night roosts with paired logistic regression, a method only rarely used in biology. This method enabled us not only to describe characteristics of night roosts, but also to investigate any preferences for night roosts. The results suggest that the selection of night roosts is determined by energy saving strategies. Thus we confirmed findings in the literature demonstrating that the energy budget is a limiting factor in capercaillie winter ecology (see below).

It is well known that animals can suffer from being flushed, especially in winter. During our field work searching and sampling droppings for paper II, IV and V, we occasionally detected and incidentally flushed capercaillie. Unfortunately, the low visibility in forests did not allow to detect and

observe shy animals, or to measure alert distances (Blumstein et al. 2003). However, we were able to measure flushing distances of accidentally flushed birds during the sampling of droppings and during radio-tracking birds (paper III). By searching for droppings off-trail, we imitated an unpredictable disturbance source. Thereby we investigated a direct and local-scale behavioral response of capercaillie to a recreationists. The radio-tracking study (paper IV) mainly focused on capercaillie habitat use in relation to predictable recreation activities along ski-tracks, ski-runs and trails. Thereby, we investigated capercaillie behavioral responses to predictable (paper IV) and unpredictable (paper III) human activities. The results of this study on flushed capercaillie indicated that capercaillie did not accustom to off-trail (unpredictable) disturbances as suggested for other species (Miller, Knight & Miller 2001). This is of great conservation importance, and helps to justify regulations for recreationists not to leave designated trails or tracks. However, the radio-tracking study confirmed that capercaillie did not abandon home ranges that were partly used for human winter recreation. Recreation activities in our study did not influence the location of capercaillie home ranges within a certain area (paper IV), and home range locations did not shift with the beginning of the ski season.

We conducted two behavioural studies (flushing distances and spatial behaviour), and two physiological studies (small scale and large scale). By applying different methods to measure responses of animals to recreation, and applying these methods at different spatial and temporal scales had many advantages. First, we could distinguish between disturbances, which resulted only in a behavioral, only in a physiological response, or in both. It was particularly important to detect animals that were physiologically stressed, but did not show a behavioral response. Second, to propose successful management plans aiming at reducing disturbance-effects on capercaillie, it is important to know the relevant scale at which capercaillie are affected by winter recreation.

A critical point when studying effects of winter recreation on capercaillie is the simultaneous increase of winter recreation and change in capercaillie habitat such as increasing snow depth or decreasing ambient temperatures. The question remains, whether the decrease of capercaillie home range size during the winter is caused by increased recreation intensity or by increased snow depth affecting capercaillie food sources. Therefore, future studies should include control areas without recreation activities. Because we were able to statistically control for temperature as a determinant of stress hormone level, we could demonstrate that both low temperatures and high recreation intensities can independently lead to an increase in stress hormone level. However, the generally higher stress hormone level of capercaillie during the ski season, even in undisturbed sites, can be caused by environmental conditions independently of recreation (paper IV).

New insights in the disturbance biology of capercaillie

Capercaillie are considered to be highly susceptible to human disturbance, which could have contributed to the rapid population declines in the last decades (Storch 2000a; Storch 2000b). Some case studies documented a decrease in capercaillie number in local populations after an increase in recreation intensity (Brenot, Catusse & Ménoni 1996). This is the first study investigating effects of winter recreation on capercaillie at an individual level. There is good evidence from our studies on behavior and physiology that capercaillie are sensitive to winter recreation, and that the effects of disturbances can be harmful for the birds: (1) Capercaillie do not get accustomed to unpredictable

disturbances, since they were flushed at longer distances in areas with high recreation intensities than in undisturbed areas. (2) Capercaillie used areas with recreation-facilities before the start of the ski season, but avoided them when they were intensively used during the ski season. (3) During the ski season, capercaillie preferred undisturbed areas and avoided areas with high recreation intensity within their home ranges. (4) Fecal corticosterone metabolite concentration in areas with moderate or high recreation intensity was higher than in areas with low recreation intensity. (5) Under certain environmental conditions, fecal corticosterone metabolite concentration increased with decreasing distance to disturbance sources.

A great advantage of this study was the simultaneous use of methods investigating behavioral and physiological effects of recreation, in paper IV even measured on the same individuals. Thereby we found that capercaillie did not avoid areas with high recreation intensity before the ski season started, although capercaillie using such areas were physiologically stressed. It was important to carefully observe the onset of the ski season to study potential effects of human recreation. Therefore, we sampled droppings from radio-tracked capercaillie before and during the ski season, and analyzed data of flushed birds during and after the hunting season. Interestingly, most behavioral parameters markedly changed with the beginning of the ski season (paper IV) or the end of the hunting season (paper III). However, the physiological stress response to winter recreation intensity was always apparent over the entire study period (paper IV). Besides the temporal scale, the spatial scale was also of great importance. Winter recreation intensity had no effect on capercaillie habitat use at the large spatial scale (home ranges within study area), but at the small spatial scale (locations within home ranges).

Several studies showed that capercaillie adapt their behavior to minimize energy expenditure in winter (Gjerde & Wegge 1987; Storch 1995), since the balance of the energy budget is limited by harsh environmental conditions and by limited energy intakes. Our results point in the same direction: (1) Night roost selection in winter was determined by energy saving strategies (paper II). (2) Spatial activity of capercaillie in mid- and late winter (during the ski season) was reduced compared to early winter with less demanding environmental conditions (before the ski season). (3) Several findings showed that the behavioral (paper III, IV) and physiological (paper IV and V) stress responses of females were less pronounced or at a lower level than those of males. These results could be explained by the tighter energy budget of females, and by their higher tolerance for stress. We conclude that the strongly limited energy budget and the large body size of capercaillie are the main causes for their high susceptibility to disturbance caused by human winter recreation.

Implications for capercaillie conservation

Our results showed that winter recreation activities indeed caused behavioral and physiological stress responses in capercaillie. Although we could not investigate fitness consequences of such stress responses, adverse effects on fitness are very likely. Other studies demonstrated that human disturbance can negatively affect body condition (Lucas *et al.* 2006), energy expenditure (Cassirer, Freddy & Ables 1992), reproduction (Yasue & Dearden 2006), mortality (Müllner *et al.* 2004), and immune response (Amo, Lopez & Martin 2006). Such fitness costs have the potential to result in a local population decline. Although knowledge on disturbance-caused fitness costs is lacking in

capercaillie, we suggest that recreation in winter is an additional factor leading to local population declines. Recreation activities in summer are supposed to be less critical, since the energy budget is less tight, and additional ground vegetation increases hiding possibilities. We suggest that capercaillie remain in recreation areas despite possible negative fitness consequences because of the outstanding forest structure and the lack of suitable habitats nearby.

Various recreation activities occur in many central European capercaillie habitats. There is strong evidence that capercaillie are negatively affected by recreation activities. Therefore, the management of recreation activities in capercaillie core areas is important. I recommend three main strategies to reduce negative effects of human recreation on capercaillie.

- reduce unpredictable (off-trail) recreation activities
- ensure undisturbed forest patches without human access as refuges
- restrict day-round and intensively used facilities with noisy activities

There are several possibilities to implement such strategies. In general, the development or enlargement of recreation areas where capercaillie occur should be avoided. Regulations for recreationists to stay on trails, roads, ski-tracks or ski-runs would reduce unpredictable disturbances to which wildlife cannot adapt. Especially off-trail snow-shoeing in capercaillie forests should be restricted to trails. Inter-trail distances should exceed 100 m to avoid the flushing of capercaillie from recreationists (paper III). Trails may even have to be closed where undisturbed capercaillie core areas are strongly reduced by dissecting trails. To reduce the degree of visibility between capercaillie and recreationists, evergreen conifer trees may be planted or preserved in a dense row along critical parts of potential disturbance sources. Some parts of capercaillie habitat are without human access and function as important disturbance-free refuges, often due to topographic barriers such as steep slopes, rocky areas or avalanche runs. In areas easily accessible for humans, such disturbance-free refuges need to be created by the establishment of officially declared wildlife refuges with prohibited access. Intensively used recreation facilities with frequent and noisy activities, such as tourist lodges, car parks or biathlon shooting stands, should be avoided in capercaillie core areas.

Capercaillie have received great attention by nature conservationists and land managers in the last years. Several extensive capercaillie conservation programs in central Europe aim to stop population decline by increasing habitat quality, controlling capercaillie predators or marking deer fences and wires to reduce collisions (Baines & Andrew 2003). Compared to these conservation measures, the regulation and control of recreation activities in capercaillie core areas seem to be less cost intensive. The management of recreation should be part of management plans for capercaillie conservation. Great care has to be taken to avoid the failing of expensive habitat management efforts because of a lack of recreation management. The incentive to increase suitable capercaillie habitat by the management of recreation activity is given, since capercaillie is an umbrella species (Suter, Graf & Hess 2002) enabling other species to benefit from such management efforts.

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Acknowledgments

First of all, I would like to thank Lukas Jenni and Susanne Jenni-Eiermann for all their support during the last three years. I highly appreciated their critical reading and commenting to substantially improve the manuscripts and their generous help during all the stages of this study. I thank for the opportunity to visit several conferences during this thesis.

I am grateful to Rupert Palme and his collaborators at the University of Veterinary Medicine in Vienna, who supported and facilitated the validation study and introduced me into the laboratory work.

I thank Christine B. Müller, Rupert Palme, Bernhard Schmid and Ilse Storch for acting as external examiner of my thesis.

My gratitude goes to the entire team of colleagues who helped me with an excellent field work including capercaillie trapping, tracking and dropping sampling under hard environmental conditions (Batist Bischoff, Dölf Egenter, Samuel Ehrenbold, Judith Ehrlacher, Christoph Grütter, Jonas Kleyer, Christof Elmiger, Peter Nyffeler, Emmanuel Rey, Franz Rudmann, Matthias Ritschard, Tobias Roth, Thomas Sattler, and Thomas Wicki). I also thank Kurt Bollmann, Ruedi Hess, Hannes Jenny and Sébastien Sachot and their collaborators for their valuable support to enable a successful field work, and Philip Tipping for his generous editing of manuscripts.

I am especially grateful to Ruedi Meier for his enormous and motivating cooperation and support in the field and in the laboratory during many weeks, and to Wolfgang Ebser for his sympathy, enthusiasm and collaboration to better understand this mystical forest grouse.

I thank the project partners Rudi Suchant, Vero Braunisch, Judith Ehrlacher from the „ Forest Research Institute of Baden-Wuerttemberg FVA “, Peter Berthold, Gernot Segelbacher, Manfred Lieser, Wolfgang Fiedler, Andreas Schmidt and Uli Querner from the Max Planck Institute for Ornithology/Vogelwarte Radolfzell, the team from the “Leistungszentrum Herzogenhorn” and many more people from the Black Forest for their friendly and open collaboration. I always visited the German study sites with great pleasure.

I also thank several colleges from the Swiss Ornithological Institute for their support during this thesis: Marc Kéry and Michael Schaub (statistics); Beat Naef-Daenzer (telemetry); Pierre Mollet, Christian Marti and Niklaus Zbinden (reviewing manuscripts).

Many thanks go to all members of the Swiss Ornithological Institute Sempach and the Institute of Environmental Sciences Zurich. The coffee breaks and social hours were good opportunities to discuss and share the pleasures and difficulties of doing a PhD.

I would also like to thank to the whole international community of grouse and grousers. The meetings were excellent and motivating opportunities to improve my knowledge and fascination for grouse ecology, conservation, as well as for nature and science in general.

Last but not least I am indebted to my family, especially to my wife Conny, for their love, patience and manifold support during the time of my PhD.

This study received financial support from the Swiss Ornithological Institute Sempach, the Janggen-Pöhn Foundation, the International Council for Game and Wildlife Conservation CIC, the Federal Office for the Environment FOEN, the Hofer-Woodhead-Foundation, the Lotteriefonds Schwyz and several private individuals.

Curriculum Vitae

Dominik Karl THIEL

Born 16th September 1975 in Zurich

Citizen of Zollikon ZH, Switzerland

4/2003 – 12/2006	PhD at the Swiss Ornithological Institute and the University of Zurich, "How susceptible are capercaillie *Tetrao urogallus* to human disturbance - a behavioural and physiological approach" Supervisors: - PD Dr. Lukas Jenni, Dr. Susanne Jenni-Eiermann (Sempach) - Prof. Dr. Bernhard Schmid, Prof. Dr. Christine B. Müller (Zurich)
06/2002 – 08/2002	Internship at University of Vancouver, Department of Forest Sciences: breeding biology of cavity-nesters and survey of reproductive success of ptarmigan
03/2002	Internship at the Swiss Federal Research Institute WSL: Field work for the research project " Dynamics of capercaillie in the Swiss Alps: metapopulation modelling at the landscape level"
04/2001 – 02/2002	Diploma thesis at the Swiss Federal Research Institute WSL and the University of Zurich "Effects of forest size and forest fragmentation on artificial ground nests in two regions of the Swiss Alps" *Supervisor*: Prof. Dr. H.-U. Reyer *Co-supervisor*: Dr. Kurt Bollmann (WSL) *Award:* Best poster award at the 9th Int. Grouse Symposium 2002, Beijing/China
01/2001 – 04/2001	Internship at the Swiss National Park (GR, Zernez): activity pattern of chamois *Rupicapra rupicapra* and enzymatic bone-taxidermy of ungulates for long-time preservation
10/1997 – 02/2002	Studies in Biology at the University of Zurich